DETERMINANTS AND CONSEQUENCES OF SOCIAL STRUCTURE IN A NEOTROPICAL PRIMATE, *CEBUS OLIVACEUS*

By

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By

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I describe and compare social interactions of female wedge-capped capuchin monkeys (Cebus olivaceus) with infants, with males, and with other females. The purpose of this study is to determine the relative importance of social and demographic parameters to the evolution of female social behavior by comparing patterns of affiliative and aggressive behavior between females and different classes of interactants. The general conclusion is that group membership and individual differences among females exert the most pervasive effects on social behavior and social structure. Females in small groups minimize interactions with other group members. Rates of association, grooming and aggression were much lower in small groups for all classes of interactants except infants. Female-female interactions

were affected by rank, relatedness, and degree to which a female withdrew from the social network of the group. Low-ranking females withdrew to the periphery of the group to avoid aggression. These females also withdrew from affiliative interactions, contrary to expectation. Reciprocal grooming sessions were concentrated among high-ranking and adult females. Low-ranking females did not reciprocate grooms, and adult females did not reciprocate grooms by juveniles. Aggressive behaviors were directed by high-ranking females toward lower ranking females. Supplantations occurred primarily during foraging periods, whereas fights occurred in nonforaging context as well. Interactions with subadult and adult males were most strongly affected by dominance ranks of males and females. Dominant males were preferred grooming partners and females associated more with this male. Females were aggressive toward subadult males, especially higher-ranking subadult males. Male aggression toward females targetted middle-ranking and young-adult females. Allomaternal interactions were more frequent, on average, in the large group. Female rank and relatedness to infant were major determinants of allomaternal carrying, association, and investigation, but female age also influenced participation. Allomaternal nursing appeared random. In large groups, increased intragroup competition increased the need to defuse group tension through assertion of dominance, affiliation and

cooperation. Females direct affiliative and cooperative behaviors toward valuable group members, those that are related or high-ranking. Females are aggressive toward group members of low value, such as peripheral females and subadult males.

CHAPTER 1

INTRODUCTION

How social relationships develop and are maintained in group-living species is a major question in the evolution of sociality (Eisenberg 1966; Alexander 1974; Wilson 1975; Wittenberger 1981; Trivers 1985). Social living may evolve to maximize advantages of groups for individuals (resource acquisition: Wrangham 1980, 1983; Koenig and Mumme 1987, avoiding predation: Hamilton 1971; van Schaik 1983) or it may be imposed as a consequence of habitat limitations (lack of breeding sites: Woolfenden and Fitzpatrick 1984; Brown 1988), or demography (minimizing dispersal mortality: Brown 1988). Because group living imposes costs on individuals such as competition for resources or mates, increased probability of disease transmission or increased conspicuousness to predators, group living can only be expected when advantages exceed the detriments. Once groups form, social behavior may evolve to enhance the original advantages of group living or to regulate competitive interactions within the group, as well as between groups (Alexander 1974). Structure based on dominance hierarchies, kinship, or reciprocity may serve to reduce aggression or

promote cooperation in a group when all animals recognize the organizing principles. Social structure is mediated through social behaviors that serve to form bonds or establish relative status between individuals in a group.

The social organization of many species of primates consists of permanent associations of females with males competing for access to or control of these females (Eisenberg et al. 1972; Greenwood 1980; Wrangham 1980). These female-bonded groups are characterized by stable relationships among individuals in definable classes of social rank, relatedness, age, etc. (Crook 1970; Dittus 1977; Hinde 1983). The social relationships among group members, as reflected in the type, frequency and quality of behaviors, define the social structure of the group (Hinde 1979). Social interactions are influenced by a number of demographic and structural effects. Survival, mortality, and fecundity schedules affect group size, age-sex structure, and patterns of kinship in a group (Keyfitz 1977; Altmann and Altmann 1979). The presence or absence of certain age-sex classes, and the number of individuals in a given class can affect the expression and frequency social interactions.

Patterns of relatedness among group members may also affect social interactions (Hamilton 1964; 1972) in many species of primates (Sade 1965; Kurland 1977; Silk 1982; Dunbar 1987; but see Jay 1963; Hrdy 1977). Individuals that direct cooperative and affiliative behavior toward close kin

rather than unrelated animals are likely to increase inclusive fitness because related animals are more likely to share genes (Brown 1988). The degree to which kinship will affect expression of social behavior will depend on the cost:benefit ratio for the action and the degree of relatedness between the interactants. For example, support of a related individual during aggression may not be costly for a high ranking female, but it might be very costly for a low ranking female.

Relationships developed among certain individuals can influence patterns of social interactions. Social relationships developed among juvenile members of a group may persist into adulthood and regulate adult social interactions (Cheney 1977; Hausfater et al. 1982). Competition for access to desirable social partners may result because animals may vary in their abilities to secure resources or to supply benefits to a partner (Seyfarth 1977; Seyfarth et al. 1978). Competition for partners and the relationships among partners should regulate social interactions within the group. Seyfarth et al. (1978) have demonstrated that, among several Old World primate species, females exhibit grooming patterns that result from competition for high-ranking partners.

This study investigates the determinants of social structure among female wedge-capped capuchin monkeys, Cebus olivaceus, Neotropical, arboreal primates. I consider the

relative importance to social structure of dominance rank, relatedness, group size, and demographic characteristics of individuals, such as age and reproductive value. These sociodemographic variables have been proposed to explain the evolution of social structure in primates. I address the question of how much variation observed in social behavior is attributable to particular parameters. I examine affiliative and agonistic social interactions among females, between females and males, and between females and infants. For each class of interactants, I ask what parameters consistently explain the suite of behaviors considered. I attempt to assess the relative importance of a parameter by determining how much of the variability in social behaviors can be accounted for by that parameter. If a variable is important in the evolution of social structure, it should be reflected over a range of behaviors. Finally, I evaluate the importance of individual differences among females in the patterns of social behavior.

CHAPTER 2

ALLOGROOMING BEHAVIOR AMONG FEMALE WEDGE-CAPPED CAPUCHIN MONKEYS: DESCRIPTION AND DETERMINANTS OF AFFILIATIVE BEHAVIOR.

Introduction

How social relationships develop and are maintained in group-living species is a major question in the evolution of sociality (Alexander 1974; Wilson 1975; Wittenberger 1981; Trivers 1985). Social living may evolve to maximize advantages of groups for individuals (resource acquisition, Wrangham 1980, 1983; Koenig and Mumme 1987, avoiding predation, van Schaik 1983; Hamilton 1972) or it may be imposed as a consequence of habitat limitations (lack of breeding sites, Woolfenden and Fitzpatrick 1984; Brown 1988), or demography (minimizing dispersal mortality, Brown 1988). Because group living imposes costs on individuals such as competition for resources or mates, increased probability of disease transmission or increased conspicuousness to predators, group living can only be expected when advantages exceed the detriments. Once groups form, social behavior may evolve to enhance the original advantages of group living or to regulate competitive

interactions within the group, as well as between groups (Alexander 1974). Structure based on dominance hierarchies, kinship, or reciprocity may serve to reduce aggression or promote cooperation in a group when all animals recognize the organizing principles. Social structure is mediated through social behaviors that serve to form bonds or establish relative status between individuals in a group.

Allogrooming behavior is a form of social communication in which relationships are developed and maintained (Sparks 1967; Seyfarth 1977; Walters and Seyfarth 1986). Allogrooming may serve as appeasement behavior by which individuals reduce tension or redirect aggression (Marler 1965; Sparks 1969). In many birds and mammals (Eisenberg 1962, 1981; Harrison 1965; Sparks 1967; Gaston 1977; Kaufman 1983) allogrooming serves to maintain dominance relationships; the dominant individual grooms. Wilson (1975) interprets the solicitation to groom as a submissive posture and Kaufman (1983) suggests that allopreening allows individuals to avoid potentially aggressive face-to-face encounters. Conclusions concerning grooming as a dominance interaction are that grooming should occur among species that are characterized by high levels of aggression and dominance hierarchies, that grooming should be directed down the hierarchy, that grooming should not be reciprocated, and that subordinate animals should withdraw from or terminate grooming. Long term consequences of grooming, such as

support during aggression, or correlation with other social behaviors are not predicted by a dominance model.

Among primates, the direction of grooming often is reversed; grooming is directed toward dominant animals (Table 2.1). This appears to be the typical pattern among female macaques and baboons (Family: Cercopithecidae). In some New World primates, however, females direct grooming down the dominance hierarchy (spider monkey, Ateles geoffroyi and mantled howler monkey, Alouatta palliata). Evidence exists to support the hypothesis that grooming serves to maintain dominance relations through appeasement. In Cebus albifrons, a reciprocal relationship between grooming and aggression was interpreted as evidence of the role of grooming in maintaining social structure (Berstein 1965), supporting Wilson's (1975) observation that in short term interactions, aggression and grooming are inversely related. Schino et al. (1988) provide behavioral evidence that grooming reduces tension (as measured by a reduction in displacement activities in Java macaques (Macaca fascicularis) and Boccia (1987) provided preliminary physiological evidence that receiving grooming reduced tension as measured by heart rate monitoring. Appeasement, however, is not sufficient to explain grooming patterns other than dominance relations, nor does appeasement contribute to understanding social interactions that are correlated with grooming.

Table 2.1. Sample of lemurs, New World and Old World primates indicating relationship between dominance hierarchy and direction of grooming.

Species	Female dominance hierarchy	Direction of grooming	Reference
Indri indri	yes	?	Pollock 1979
Lemur catta	yes	none	Budnitz and Dainis 1975
Alouatta seniculis	yes	?	Saavedra 1984
Alouatta palliatta	yes	down	Jones 1979
Ateles geoffreyi	yes	down	Eisenberg and Keuhn 1966
Saimiri sciureus	none	none	Baldwin and Baldwin 1981
Saguinus oedipus	yes	?	Dawson 1978
Cebus olivaceus	yes	down	this study
Colobus guereza	none	none	Oates 1977
Colobus badius	none	none	Struhsaker 1975
Presbytis entellus	yes	none	Hrdy 1977
Erythrocebus patas	?	none	Hall 1965 Rowell and Hartwell 1978
Cercopithecus ascanius	none	none	Cords 1986
Cercopithecus campelli	none	none	Cords 1986
Cercopithecus mitis	none	none	Cords 1986
Cercopithecus aethiops	yes	up	Seyfarth 1980 Fairbanks 1980
Cercocebus galeritus	yes	up	Kinnaird pers. comm.
Macaca arctoides	yes	up	Rhine 1972
Macaca fuscata	yes	up	Kurland 1977
Macaca mulatta	yes	up	Sade 1972 Seyfarth 1977
Macaca radiata	yes	up	Silk 1982
Papio ursinus	yes	up	Seyfarth 1977
Papio hamadryas	yes	up	Stammbach 1978
Papio cynocephalus	yes	up	??
Theropithecus gelada	yes	up	Kummer 1975
Gorilla gorilla	yes	none	Stewart and Harcourt 1986
Pan troglodytes	yes	?	Nishida 1979
Pan paniscus	none	none	Kuroda 1980

Allogrooming also may act as currency in reciprocal relationships with long-term consequences (Seyfarth and Cheney 1984; Walters and Seyfarth 1986). A theory based on reciprocity incorporates a broader array of relationships than a theory based only on appeasement and is especially useful for long-lived social species such as primates. Grooming relationships in primates may reflect dominance or sexual relationships (male-female grooming), close genetic relatedness (mother-offspring grooming), and individual differences in attractiveness (Seyfarth et al. 1978). Mothers with infants and high-ranking females, for example, have been shown to be especially attractive in different studies (Walters and Seyfarth 1986).

Seyfarth (1977) explored the causal roles of rank, attractiveness and relatedness in a model that predicted social-grooming networks among adult female primates. Seyfarth observed that, among unrelated females, attractiveness is directly related to rank, and that access to attractive partners may be restricted by competition (dominance relationships). He noted, furthermore, that in many primate species, closely related females often occupy adjacent ranks and that preference for grooming relatives is reinforced by dominance and attractiveness. The interaction between preference based on rank and preference for close kin, may explain the common features of grooming networks for a wide variety of species. His model predicts that

females are attractive as a direct function of their rank, that females are selected to maximize interactions with high-ranking females, and that competition for access will result in compromise that determines the exact distribution of grooming partners. Concerning the direction of grooming, the model assumes that receiving grooming brings more benefits than giving grooming. Lower-ranking females will give more grooming because higher-ranking females are more attractive. Grooming imbalances will be least when females are of adjacent ranks, and competition among females will affect the relative amounts of grooming given and received.

Support for the attractiveness of high rank and the hypothesis that the majority of grooming is between adjacent ranked females comes from many analyses of grooming among macaques and savannah baboons (see Table 2.1). All tests have involved ground-dwelling cercopithicine monkeys; studies of colobines, forest guenons (also Cercopithecines) and great apes do not support the pattern. In most of these species, grooming does not follow rank patterns. Available grooming data for New World monkeys also fail to support the model. The New World examples are exceptional in that both are arboreal, forest species and are characterized by female dispersal (Crockett and Eisenberg 1986; Symington 1988). These observations suggest that the attractiveness of high rank and relatedness may be important only in species that

form female-bonded groups, or only in ground-dwelling species.

Forest species, such as the wedge-capped capuchin monkeys (Cebus olivaceus) are ideal subjects for testing theories of social behavior and group living. The groups are female-bonded, range in size from 5 to 40+, and have a number of matrilines within groups (Robinson 1981, 1988a, b). The groups have stable matrilineal dominance hierarchies. Capuchin monkeys are highly social; aggressive and affiliative interactions occur commonly. Capuchin monkeys are arboreal, but spend most of the day within 20 m of the ground and observation conditions are excellent. Previous work has shown the benefits of group living in relation to access to resources, vigilance for predators, and reproductive success of males and females (Robinson 1981, 1986, 1988a, b; de Ruiter 1986; Srikosamatara 1987). A rank-related cost of group living for females also has been documented (O'Brien 1988).

This study addresses the questions of how female capuchin monkeys maintain affiliative relationships and what are the determining sociodemographic factors underlying grooming relationships. I examine how females participate in grooming, the structure of grooming sessions, and the effect of age, rank and relatedness on grooming relationships. I next test the Seyfarth model and discuss the relevance of the model to non-cercopithicine primates.

Study Area

The wedge-capped capuchin monkey occurs in the llanos of Venezuela, a 200,000 km^2 region in the central lowlands. Capuchins inhabit dry deciduous and gallery forests along rivers and streams, and scrub forests (matas). Proximity to permanent water is an important aspect of the wedge-capped capuchin monkey's home range during the dry season (Robinson 1986) The study area is located on Fundo Pecuario Masaguaral, a 3,000 ha cattle ranch maintained as a wildlife management area since the 1940s. The ranch is located in the state of Guarico in the central llanos, 50 km south of Calabozo, 8° 34'N, 67° 35'W. My study site is a 300 ha gallery/dry deciduous forest, and a 200+ ha area of broken scrub forest. The climate is strongly seasonal with a 4-month dry season (December-March), a 6-month wet season (May-October) and 2 transitional months (April and November). Vegetation characteristics have been described by Troth (1979) and Robinson (1986).

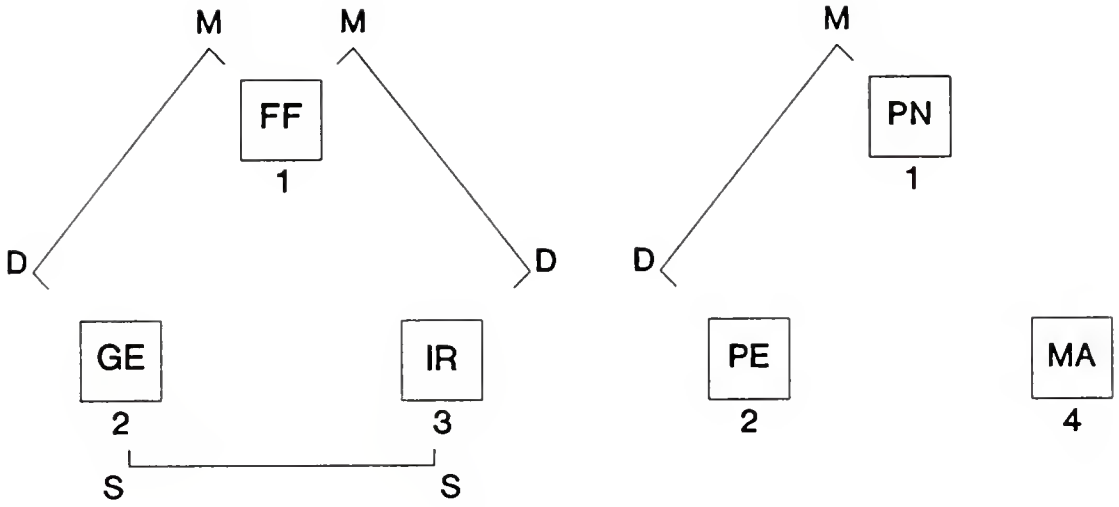
Methods

I studied 7 females in 2 small groups and 12 females in 1 large group of wedge-capped capuchin monkeys. White group ranged from 7 to 10, Splinter group ranged from 9 to 11, and Main group ranged from 21 to 26 individuals over the course of the study. One adult female migrated into White group during the study, but stayed for only 3 months and rarely interacted with the other females. I excluded this female

from the analysis. One Main group female disappeared near the end of the study. This female was included in the analysis. Dominance hierarchies and geneologies were known for all groups (Fig. 2.1) and all individuals were recognizable by facial differences, and by variation in pelage, body size, and habit. The 3 groups yielded 3, 6, and 66 pairs of females (dyads) that could potentially interact. I eliminated grooming among juveniles because there were only 3 dyads present. Analyses of grooming relationships among females therefore included 72 possible dyads.

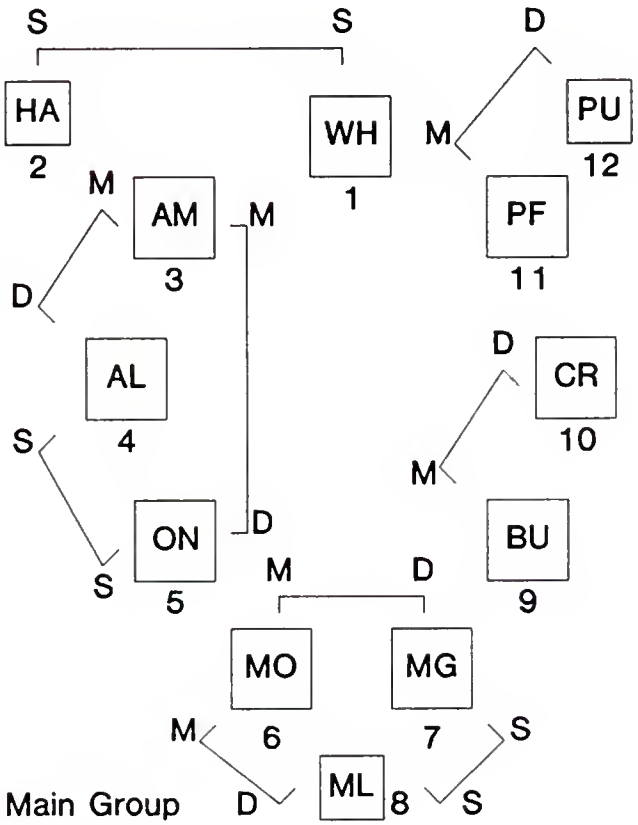
I collected data for 15 months (December 1986 to March 1988, no data collected in June 1987). Daily behavioral observations began between 0600 and 0630, and lasted for 12 hours. Observations consisted of a 20-minute focal sample on an individual female, followed by a 20-minute scan sample of the group, and a 20-minute opportunistic sample each hour (Altmann 1974). Females were sampled systematically such that each female was included in a focal sample in each of three 4-hour time periods (morning, midday, and late afternoon). During the first 12 months of sampling, I recorded all behaviors that lasted at least 3 seconds during a focal sample. For the last 3 months I recorded only social interactions that were defined as affiliative or agonistic interactions involving 2 or more individuals. During the scan sample, the behavior and nearest neighbor of each group member were noted.

Figure 2.1. Rank and close kin (r=0.5) relationships among females in 3 study groups. Ranks are indicated by numbers and Rank declines in counterclockwise direction. Mother-daughter (M-D) and sibling (S-S) relationships are indicated by brackets. In Main group, adult females are positioned on inner ring and juvenile females are positioned outside the ring.



White Group

Splinter Group



Main Group

During opportunistic samples, I recorded all observed social interactions involving females. I minimized observation bias by moving constantly through the group looking for social interactions. Because viewing conditions were excellent, I probably missed very few social interactions. I tested the frequency that individual females were involved in grooming sessions (using Chi-square test; Sokal and Rohlf 1981), the amount of grooming in a session and duration of grooming sessions (two-sample T-tests; Sokal and Rohlf 1981) in the focal and opportunistic samples. There were no significant differences in the frequency of grooming sessions, amount of grooming during a session, or duration of a grooming session between the 2 samples. Because the data sets were comparable, I combined data from focal and opportunistic samples for analysis.

For each grooming session I recorded the identities of interactants and the frequency and duration of each behavior lasting more than 3 seconds (Table 2.2). Grooming sessions were initiated when a female approached a soliciting or stationary female and one party began grooming, or when 2 females already in close proximity began grooming. Grooming sessions always included at least 1 grooming event; solicitations without grooming interactions were not included. Grooming sessions were terminated when one or both animals moved away, when one animal failed to reciprocate a groom or respond to a solicitation for more than 30 seconds,

Table 2.2. Description of behaviors associated with grooming sessions.

Agonistic Support. Coalition formed to assist in aggressive encounters against other males or females.

Approach. Moving toward another individual. Approaches usually result in a social interaction, either aggressive or affiliative.

Solicit. An invitation to another animal to groom. Animal lies down on its side with its back to target animal. Alternatively, during grooming, animal may sit facing grooming partner and raise arms and head upwards (sky-point).

Groom. Manipulating fur and skin of another individual with fingers, mouth and teeth to remove bits of dirt, dead skin, ectoparasites, blood from wounds, etc.

Grooming Session. The time spent in close proximity during which grooming occurred.

Termination. Cessation of grooming due to lack of response to solicitation, failure to reciprocate on a groom, or one or both individuals leaving the session.

Reciprocated Grooming. Both individuals groom in a single session.

or when one or both animals engaged in 1 or more asocial behaviors for more than 30 seconds but remained in close proximity. A grooming session, therefore, included time spent in close proximity as well as time spent grooming.

I considered 3 data sets: (1) the individual grooming sessions between pairs of females (2) the summary of grooming relationships between each pair of females and (3) the summary of each female's participation in grooming irrespective of partner. I use the individual grooming sessions to describe the dynamics of grooming among females, the fluctuation of grooming over time, the effect of a female with a new infant on grooming sessions and to evaluate reciprocity in grooming. The summary data for grooming dyads to determine the effects of age, rank and relatedness on grooming relationships, what aspects of grooming are general and what factors might influence strong grooming relationships. The data summarizing each female's participation in grooming incorporate a set of counts, proportions and ratios (Table 2.3) that measure a female's participation in grooming sessions and distinguish how females vary in their relationships with other females.

I considered duration of grooming session, time spent grooming by each participant in a session, and the frequency of grooming sessions as the basic data for the analysis of individual grooming bouts and for the analysis of grooming relationships. Grooming sessions were classified as

Table 2.3. Identification and characteristics of female wedge-capped capuchin monkeys involved in grooming sessions.

Identity	Group	Age	Rank	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
FF	White	A1	H	0.57	21	3.41	0.57	0.33	0.56	0.43	0.19
GE	White	A2	M	0.14	13	3.53	2.20	0.63	0.38	0.62	0.08
IR	White	A1	L	0.29	11	2.46	1.26	0.40	0.30	0.83	0.36
PN	Splinter	A	H	0.40	12	2.14	1.95	0.27	0.11	0.57	0.33
PE	Splinter	J	H	0.27	29	3.22	3.63	0.62	0.11	0.30	0.07
RO	Splinter	A1	M	0.00	16	2.95	0.46	0.17	0.35	0.60	0.50
MA	Splinter	A1	L	0.33	31	3.17	0.36	0.15	0.54	0.75	0.35
WH	Main	A	H	0.87	98	3.13	1.83	0.58	0.27	0.37	0.03
HA	Main	J	H	0.58	67	2.01	2.24	0.48	0.45	0.44	0.19
AM	Main	A1	H	0.30	129	2.59	0.56	0.33	0.52	0.64	0.48
AL	Main	A2	H	0.75	76	2.45	1.52	0.39	0.51	0.36	0.18
ON	Main	A2	M	0.62	66	2.38	1.66	0.62	0.52	0.47	0.12
MO	Main	A1	M	0.06	51	2.48	0.18	0.37	0.69	0.79	0.55
MG	Main	A2	M	0.50	36	3.65	2.53	0.50	0.26	0.27	0.17
ML	Main	J	M	0.64	31	2.84	0.55	0.43	0.42	0.34	0.23
BU	Main	A	L	0.33	12	1.80	0.39	0.67	0.45	0.58	0.75
CR	Main	A1	L	0.23	32	2.00	0.11	0.00	0.55	0.79	0.75
PF	Main	A	L	0.20	20	1.74	1.05	0.30	0.57	0.50	0.50
PU	Main	J	L	0.50	12	1.83	0.33	0.33	0.50	0.40	0.33

Notes on column headings: Age - A1=adult, infant born during study; A2=adult nulliparous; A=adult, multiparous; J=juvenile. Rank - H=high, M=medium, L=low. (1) proportion of approaches initiated by ID. (2) number of grooming sessions. (3) mean duration of grooming session. (4) ratio of grooming given to grooming recieved, in minutes. (5) proportion of solicits responded to by ID. (6) proportion of solicits by ID that were responded to by grooming partner. (7) proportion of grooming sessions terminated by ID. (8) proportion of grooming sessions in which ID did not reciprocate grooming.

reciprocated or unreciprocated, depending on whether both participants groomed. Sessions also were classified into 3 categories based on the presence and age of infants belonging to at least 1 of the interactants (0 = no infants, 1 = infant <1 month old, 2 = infant 1-2 months old. Participants were classified by age (juvenile and adult) and by rank (high, medium and low). Within a rank class, the first individual identified was always the higher-ranking individual of the dyad. In this way, rank relationships within a rank class were preserved in the relative amounts of grooming between participants. Degree of maternal relatedness ($r = 0.5, 0.125, 0$) between participants was noted and all values of $r < 0.125$ were set equal to 0. Group membership was classified as large versus small.

From the basic information on grooming, a series of ratios and proportions characterizing grooming relationships can be calculated (as in Table 2.3). Asymmetry in a grooming relationship is measured by the difference in amount of grooming between 2 individuals and the ratio of grooming by one individual to grooming by the other. Response to solicitation is measured by the number of times that grooming follows a solicitation divided by the number of solicitations. Reciprocity by an interactant is measured as the proportion of grooming sessions that an individual reciprocates grooming. The proportion of sessions terminated by one or the other interactant also was calculated. Females

that have long sessions, a high grooming ratio greater than or equal to 1, high response to solicitation, high rates of reciprocity and low termination rates are expected to be good grooming partners and should have a high number of grooming sessions. Similarly, grooming relationships that are balanced in response to solicitation, grooming, termination and reciprocity, should be stronger (more grooming sessions) than relationships in which one partner does all the grooming.

I used both parametric and nonparametric analyses. When sample sizes were large, ANOVAs were complex, or when tests of distributions were appropriate, I used parametric analyses such as repeated measures ANOVA and Chi-Square tests (Sokal and Rohlf 1981). Nonparametric Rank Sum tests, Wilcoxon Sign Rank tests, and Kruskal-Wallis 1-way ANOVA were used for testing differences in grooming attributes of individual females and testing differences in patterns of grooming as a function of relatedness (Hollander and Wolfe 1973). All analyses were performed on the SAS statistical package (SAS 1985).

Results

Characteristics of Grooming Sessions

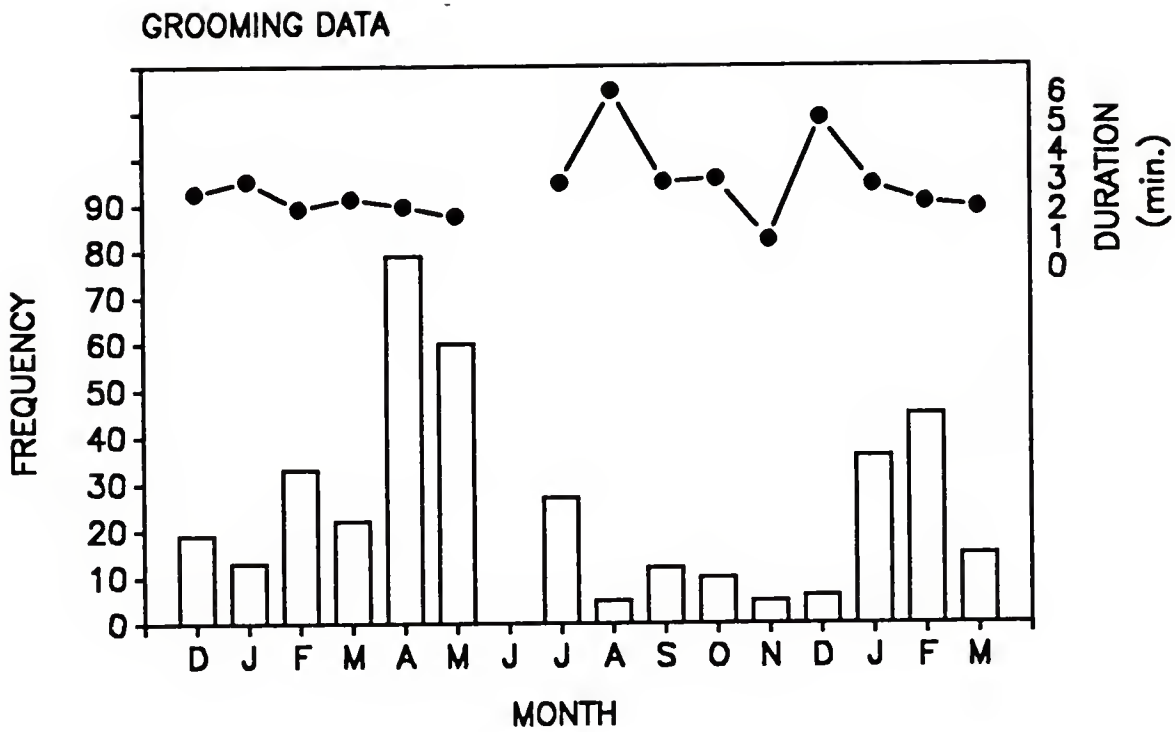
Grooming sessions between females occurred 384 times during the course of the study. The average grooming session lasted 2.51 minutes (SE=0.134) with the higher-ranking female grooming an average of 1.14 minutes and the lower-

ranking female grooming for 0.71 minutes. Frequency of grooming varied considerably by month (mean=25.80, SE=5.59; Fig. 2.2) with minor peaks in February and a major peak in April-May when infants appeared in Main group. Monthly mean duration of grooming stayed relatively constant over time. The largest deviations in durations occurred in months with the least grooming (August, November, December) and are probably the result of small sample size.

Several behaviors and behavioral sequences associated with grooming sessions were noted. Of 173 approaches that did not result in supplantation or aggression, 100 approaches were associated with grooming sessions. Other sessions were initiated after animals were in proximity but engaged in asocial behaviors or after an animal had been following another. High-ranking animals initiated most approaches (65%) and approached high-ranking animals more often than low ranking animals. If a low-ranking animal approached a higher-ranking animal, the higher-ranking animal was usually related or of a similar rank. Very low-ranking animals rarely approached high ranking animals. Adults usually approached adults rather than juveniles. Generally, relatedness was not an important factor in approaches.

Approaches were often toward soliciting females (20 records) or toward a female that responded to the approach

Figure 2.2. Frequency and mean duration of grooming sessions by month for female wedge-capped capuchin monkeys.


GROOMING DATA
FREQUENCY
90
80
70
60
50
40
30
20
10
0
6
5
4
3
2
1
0
DURATION
(min.)
D J F M A M J J A S O N D J F M
MONTH

by soliciting (23 records). In 30 approaches the approaching female then solicited a groom. The most common outcome of an approach was immediate grooming (no solicitation or solicitation lasting less than 3 seconds) of the female being approached. Solicitations, in all contexts, resulted in grooming only 44% of the time. The behavior was often ignored, met with a solicitation, or the target moved away.

Ignoring a solicitation, moving or failing to reciprocate grooming terminated the session. The lower ranking member of the session was responsible for termination in 218 of 373 sessions. In 47 of 72 dyads, the lower-ranking female terminated more sessions than the higher-ranking female. This pattern was consistent except when medium-ranking females were grooming medium- or high-ranking females. In these dyads, the higher-ranking animal tended to terminate more often. Among adult females, the lower-ranking female terminated more, but between adult and juvenile females, both parties were equally likely to terminate. Among unrelated females, the lower-ranking female terminated more, whereas among closely related females ($r=0.5$), both females were likely to terminate.

The Influence of a Newborn Infant

To determine the importance of the presence of young infants to frequency and duration of grooming, I analyzed the amount of grooming per month for 15 adult females of different ranks in large and small groups as a function of

the presence of infants (none, 0-1 month old infant, 1-2 month old infant). Juveniles were excluded from the analysis because they could not bear infants. I used repeated measures ANOVA (Sokal and Rohlf 1981) that treated rank and group as blocks and presence of infant as a treatment.

The duration of grooming was unaffected by group size, female rank or the presence of an infant. Frequency of grooming sessions was significantly higher in the large group (4.1 vs 1.4 sessions/month; Table 2.4; Fig. 2.3). High-ranking females were involved in grooming sessions significantly more than middle- and low-ranking females (4.9 vs 2.6 and 1.7 sessions/month respectively). Females with new infants were involved in significantly more grooming sessions than females with 1-month old infants and females with no infants were involved in the least amount of grooming (16.0, 6.2 and 2.7 sessions, respectively). Variability among females was substantial (interaction terms, Table 2.4; Fig. 2.4). Females in small groups did not respond strongly to rank differences, or to the presence of infants. Grooming declined with rank for females with new infants and females with no infants but not for females with 1-month old infants. However, 2 important data points in this comparison have sample sizes of 1, and this result should be treated as preliminary.

Table 2.4. ANOVA results for the effect of group size, rank, and presence of infant on frequency of involvement in grooming for adult females. ID is the female identity. Infant refers to the presence and age of infant.

Source	d.f.	S.S.	M.S.	F-test[1]	P>F
Group	1	492.1	492.1	51.12	0.0001
Rank	2	553.3	276.6	28.73	0.0001
Group x Rank	2	211.6	105.8	10.99	0.0001
ID(Group x Rank)	9	86.6	9.6	0.99	0.4520
Infant	2	997.2	498.6	51.14	0.0001
Infant x Group	2	322.4	161.2	16.53	0.0001
Infant x Rank	4	451.2	112.8	11.57	0.0001
Error	179	1745.2	9.7		
Total	201				

1. F-tests for Group, Rank, and Group x Rank interaction use ID(Group x Rank) as the error term. Other tests use M.S. error.

Figure 2.3. Mean and SE of frequency and duration of grooming sessions for female wedge-capped capuchin monkeys in large and small groups. Females in large groups are presented by ranks.

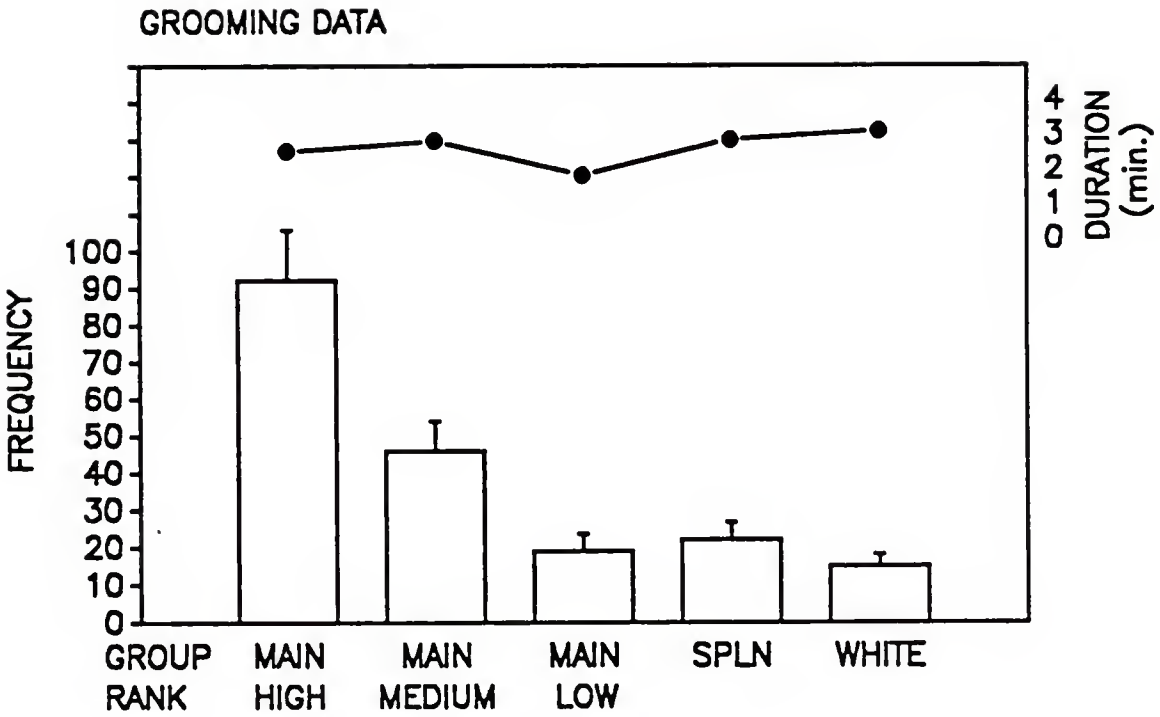
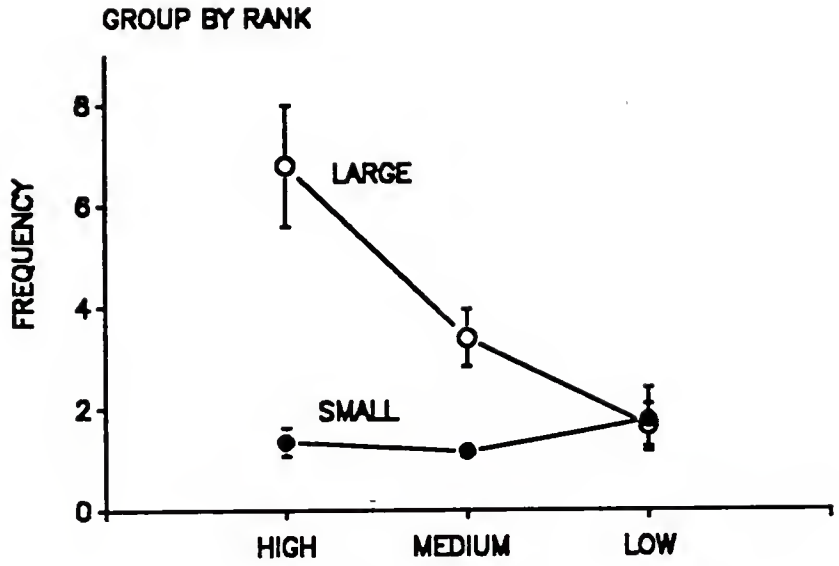
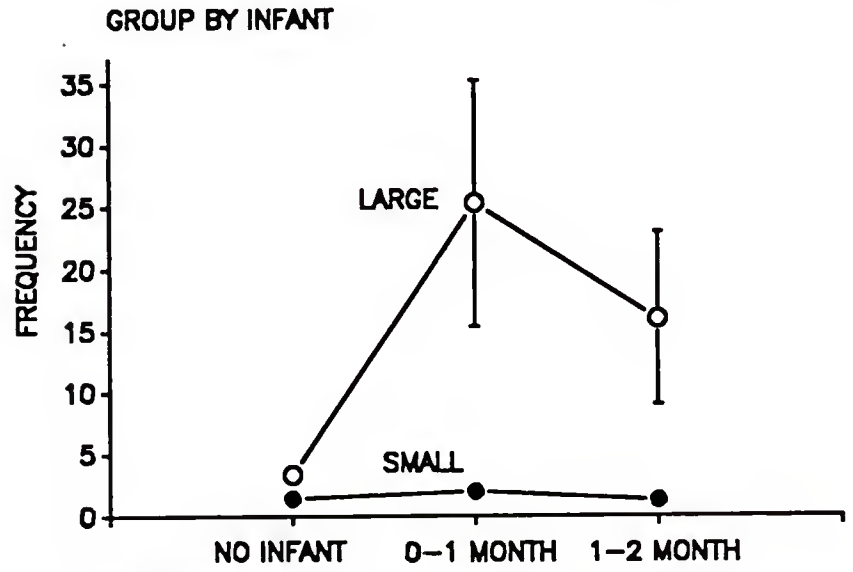
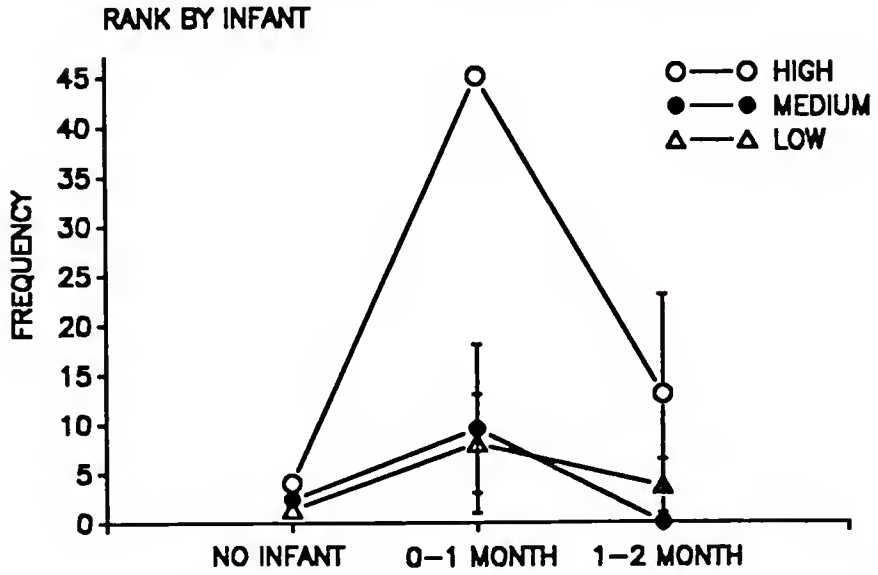

GROOMING DATA
FREQUENCY
100
90
80
70
60
50
40
30
20
10
0
4
3
2
1
0
DURATION (min.)
GROUP RANK
MAIN HIGH
MAIN MEDIUM
MAIN LOW
SPLN
WHITE

Figure 2.4. Interactions between membership in a large versus small group, female rank, and presence of infant as they affect frequency of grooming for adult females.


GROUP BY RANK
FREQUENCY
8
6
4
2
0
LARGE
SMALL
HIGH
MEDIUM
LOW


GROUP BY INFANT
FREQUENCY
35
30
25
20
15
10
5
0
LARGE
SMALL
NO INFANT
0–1 MONTH
1–2 MONTH

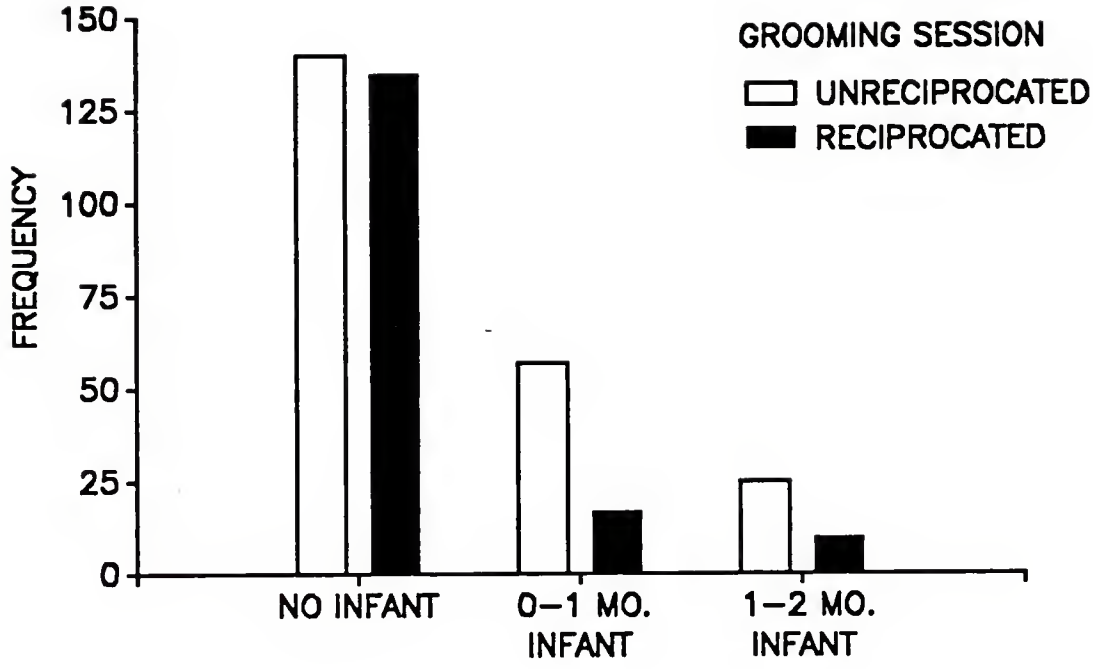

RANK BY INFANT
FREQUENCY
45
40
35
30
25
20
15
10
5
0
HIGH
MEDIUM
LOW
NO INFANT
0–1 MONTH
1–2 MONTH

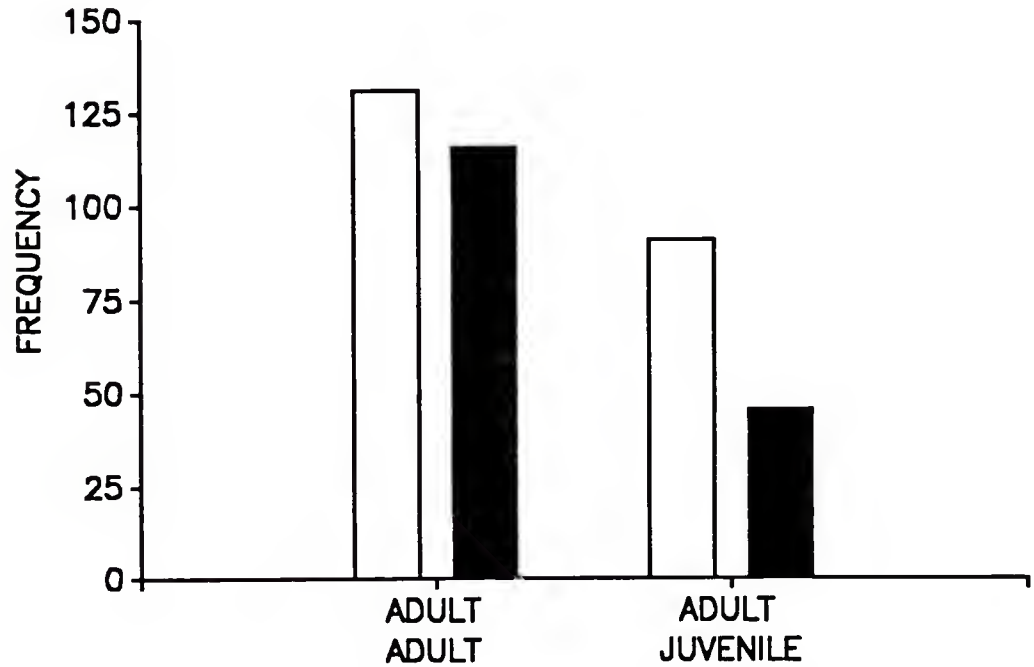
Reciprocity in Grooming

Unreciprocated grooming sessions were significantly shorter than reciprocated sessions (1.60 vs 3.75 minutes;$F=74.79$, d.f.= 3, 380, $P<0.0001$) and the total amount of grooming also was significantly less. There were no significant differences in the quality of grooming as a function of age, rank or relatedness of grooming partners between reciprocated and unreciprocated grooming sessions. Frequency of grooming did differ by age, however. Among adult females, 47% of grooming sessions were reciprocating sessions; only 33.6% of sessions involving adult and juvenile females were reciprocating (Fig. 2.5). Females reciprocate significantly more often when sessions are among adults than when sessions are between adults and juveniles (Chi-Square=6.475, d.f.=1, $P=0.0109$). In sessions with no reciprocal grooming, the lower-ranking member of the pair was the unreciprocating partner in 161 of 222 sessions.

Unreciprocated grooming was affected by the presence of new infants (Fig. 2.5). Grooming sessions when no infants were involved were as likely to be reciprocated as not. When new infants were present however, grooming sessions were 3.3 times more likely to be unreciprocated, and 2.5 times as likely to be unreciprocated when a 1-2 month old was present (Chi-Square= 19.24, d.f.=2, $P=0.0001$). Usually, the mother terminated these grooming sessions by moving away from the groomer. Quite often, however, the groomer would follow the

Figure 2.5. Distribution of reciprocated and unreciprocated grooming sessions as affected by the presence of an infant and relative ages of interactants.


150
125
100
75
50
25
0
FREQUENCY
GROOMING SESSION
UNRECIPROCATED
RECIPROCATED
NO INFANT
0–1 MO. INFANT
1–2 MO. INFANT


150
125
100
75
50
25
0
FREQUENCY
ADULT ADULT
ADULT JUVENILE

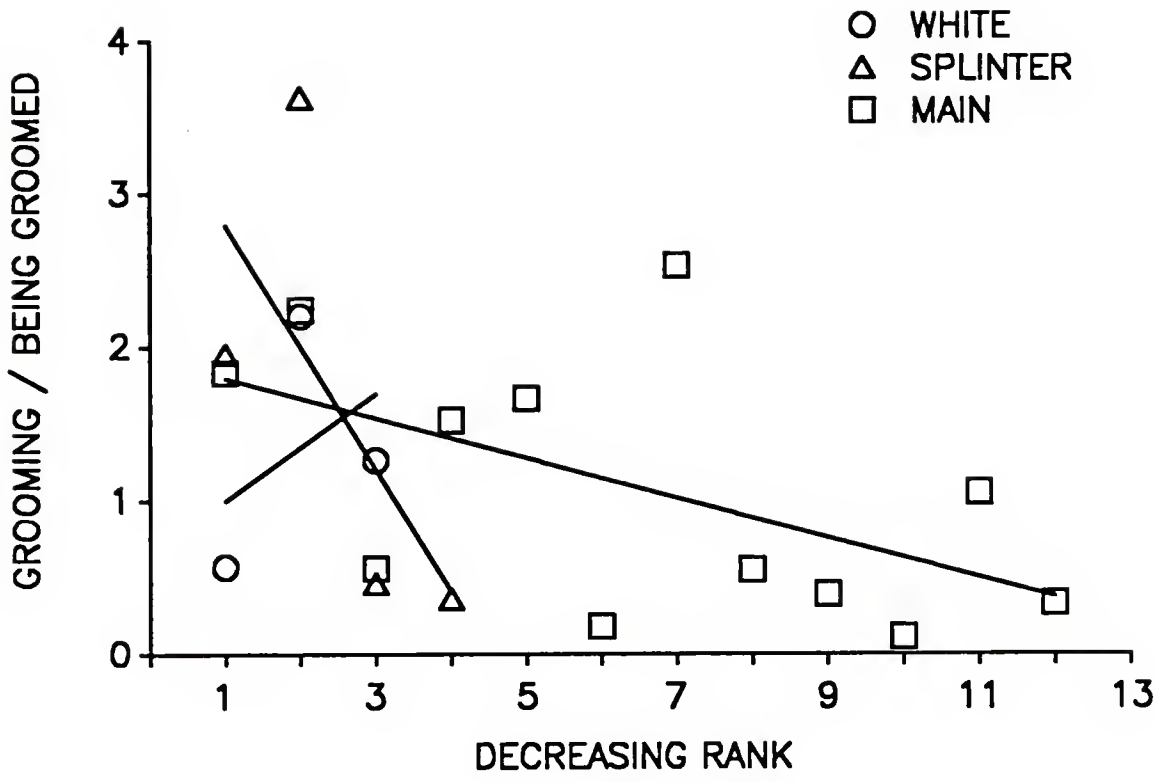
mother and another short, unreciprocated session would occur. Occasionally, a persistent groomer might follow a retreating mother 5 or more times before stopping. I interpreted these grooming sessions as attempts by a female to gain access to the infant by grooming the mother. The mother, however, appeared to withdraw from grooming interactions, especially when the infant was new.

Characteristics of Females

Grooming sessions were highly variable in structure, frequency, and duration. Much of this variability was a function of the participants (Table 2.3). High-ranking females tended to approach, respond to solicitation, and have a higher grooming ratio than low-ranking animals. Low-ranking females failed to reciprocate grooming significantly more often (50.7%; Kruskal-Wallis 1-way ANOVA, $H=6.46$, $n=19$, $P=0.0396$) than high- (21.0%) or medium- (27.5%) ranking females. Low-ranking females were less involved in grooming sessions and terminated grooming more often than high-ranking females but these difference were only marginally significant ($0.05< P <0.1$). Adult females terminated significantly more grooming sessions than juvenile females (Rank Sum test; $n=19$, $P=0.0404$).

Group differences existed in the patterns of grooming. Grooming ratios declined with rank in Main group and Splinter group, but increased with rank among closely related females of White group (Fig. 2.6; see below). Group

Figure 2.6. Ratio of giving to receiving grooming (in minutes) as a function of decreasing rank for the 3 study groups. Lines indicate trends in data for 3 groups.


WHITE
SPLINTER
MAIN
GROOMING / BEING GROOMED
DECREASING RANK
0
1
2
3
4
1
3
5
7
9
11
13

size differences were significant for frequency and duration grooming. Females in large groups groomed more frequently (large: 52.5 [SE = 10.43]; small: 19.0 [SE = 3.12]) but with much greater variability than the females in small groups ($F=19.29$, d.f.=6,11, $P=0.0008$; Rank Sum test; n=19, $P=0.0085$). Females in small groups had significantly longer grooming sessions than females in large groups although variances in duration were similar for both categories (small: 2.98 [SE = 1.93]; large: 2.41 [SE = 1.67]; Rank Sum test; n=19, $P=0.023$).

Closer examination of the frequency and duration of grooming data (Fig. 2.3) suggested that females in small groups were similar to low-ranking large-group females in the frequency of grooming but were similar to higher-ranking large-group females in the duration of grooming. Analysis of variance results confirmed that grooming frequencies were significantly higher for medium- and high-ranking females of large groups (69.25) than for low-ranking females of large groups (19) and all females (19) of small groups (Kruskal-Wallis 1-way ANOVA; $H=12.37$, $P=0.0021$). Average grooming durations for small group females (2.98 minutes) were more similar to medium- and high-ranking females of large groups (2.69 minutes) than low-ranking (1.84 minutes) large-group females (Kruskal-Wallis 1-way ANOVA; $H=9.85$, $P=0.0073$).

Grooming characteristics other than frequency and duration were associated with different females, but these

characteristics varied considerably and not always predictably (Table 2.3). Significant positive correlations existed between the ratio of grooming given to grooming received and response to solicitation, and between proportion of terminations and proportion of unreciprocated sessions (Table 2.5). Significant negative correlations existed between approach and terminate, approach and proportion of unreciprocated sessions, groom ratio and response of partner to solicitation, and response to solicitation and terminate. Females that are active in grooming sessions are females that approach, respond to solicitation, have a high grooming ratio, reciprocate grooming, and tend not to terminate grooming sessions. These characteristics tend to describe high- and middle-ranking females better than low-ranking females.

Grooming Relationships

Of all female dyads that could potentially groom with one another, 10 dyads failed to groom at all during the entire study. An additional 32 dyads groomed less than 4 times during the study. I define a grooming relationship as consisting of a minimum of 4 grooming sessions with total grooming time of at least 1 minute. In this study, 56% of the dyads failed to form grooming relationships. Failure to form a relationship followed no obvious pattern. Among closely related females, one third of the dyads fail to form grooming relationships (Figs. 2.7-2.9). Three of the 4 low-

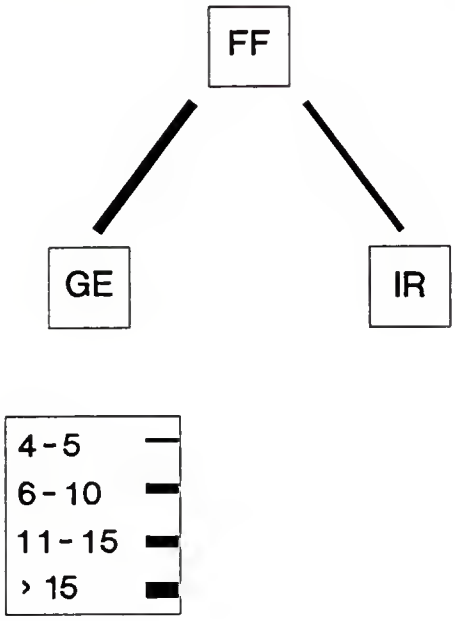
Table 2.5. Spearman rank correlation matrix for grooming characteristics of individual female wedge-capped capuchin monkeys. See Table 2.3 for definitions of variables.

	(1)	(2)	(3)	(4)	(5)	(6)	(7)
(1)	--						
(2)	NS	--					
(3)	NS	NS	--				
(4)	NS	NS	NS	--			
(5)	NS	NS	NS	0.59**	--		
(6)	NS	NS	NS	-0.72***	NS	--	
(7)	-0.64**	NS	NS	-0.53*	-0.48*	NS	--
(8)	-0.57**	NS	-0.59**	-0.71***	-0.52*	NS	0.64**

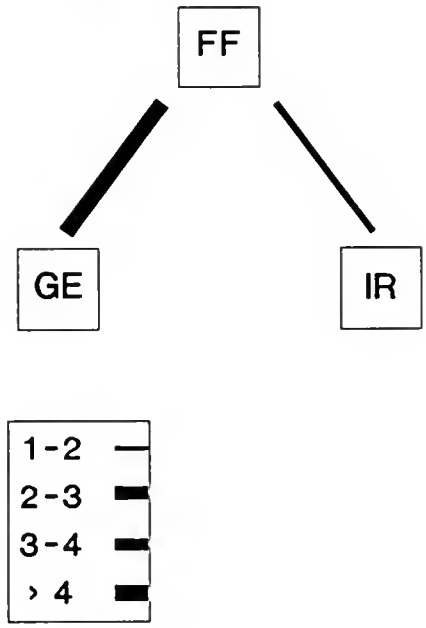
* P<0.05
** P<0.01
*** P<0.001

Figure 2.7. Grooming relationships as illustrated by number of grooming sessions, average duration and relative amounts of grooming by each member of a dyad in White group. Ordering of females as in Figure 2.1.

Number of Grooming Sessions



Average Session (min.)



Grooming Up and Down Rank (min.)

Up= Down=

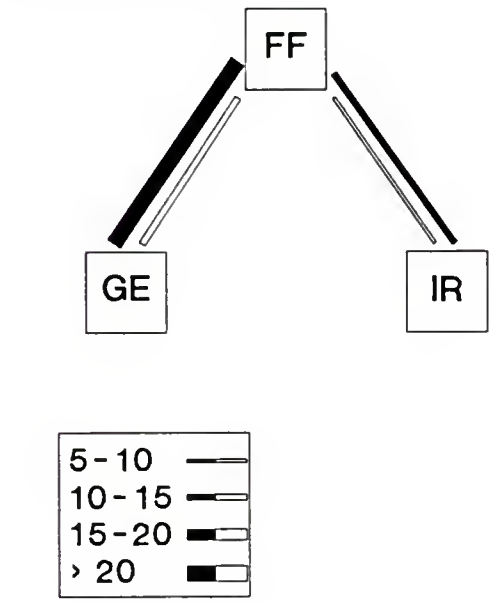
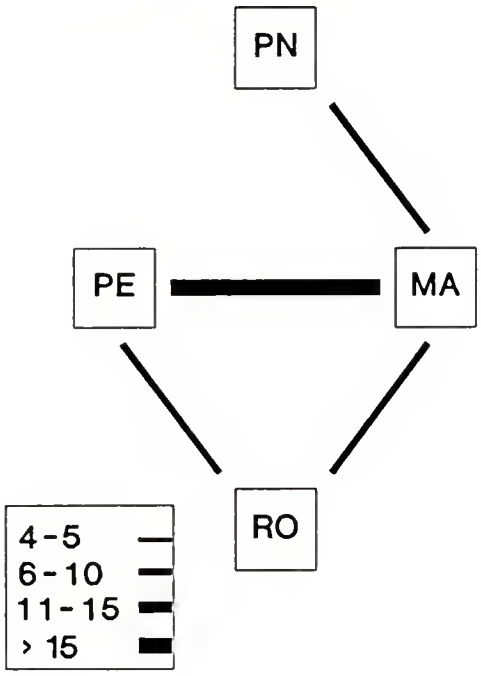
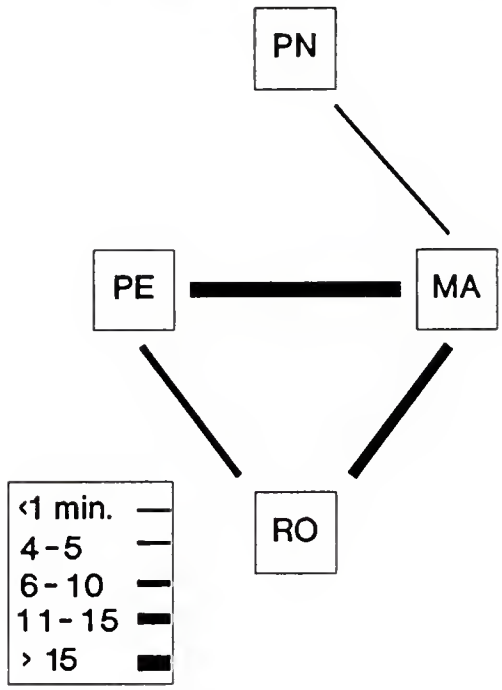


Figure 2.8. Grooming relationships as illustrated by number of grooming sessions, average duration and relative amounts of grooming by each member of a dyad in Splinter group. Ordering of females as in Figure 2.1.

Number of Grooming Sessions



Average Session (min.)



Grooming Up and Down Rank (min.)

Up= Down=

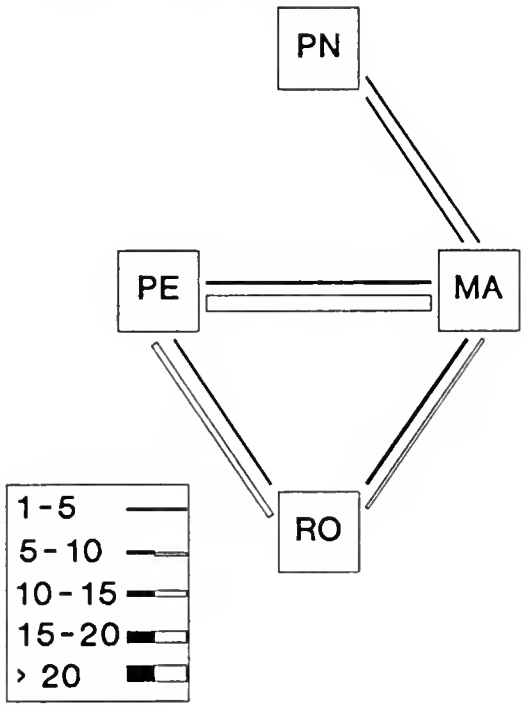
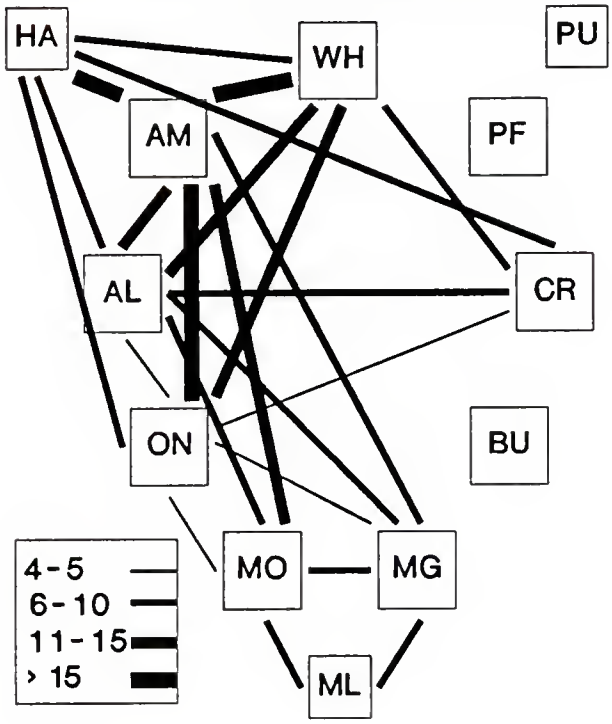
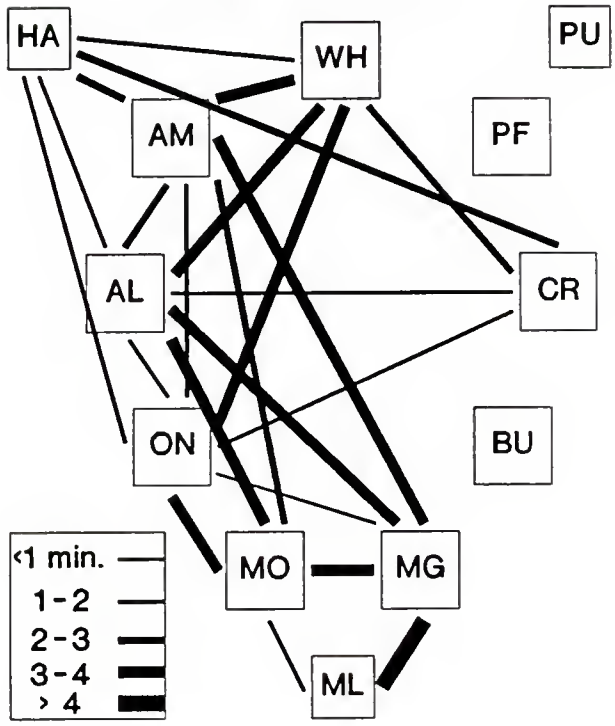


Figure 2.9. Grooming relationships as illustrated by number of grooming sessions, average duration and relative amounts of grooming by each member of a dyad in Main group. Ordering of females as in Figure 2.1.

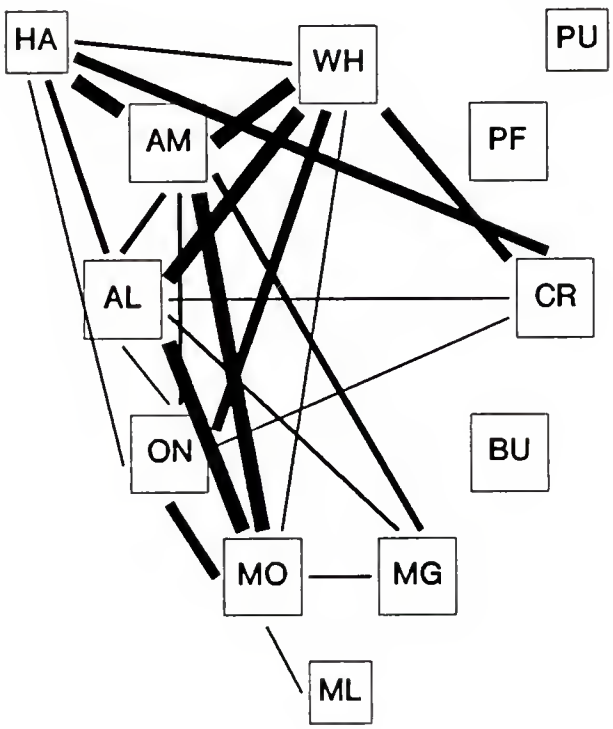
Number of Grooming Sessions



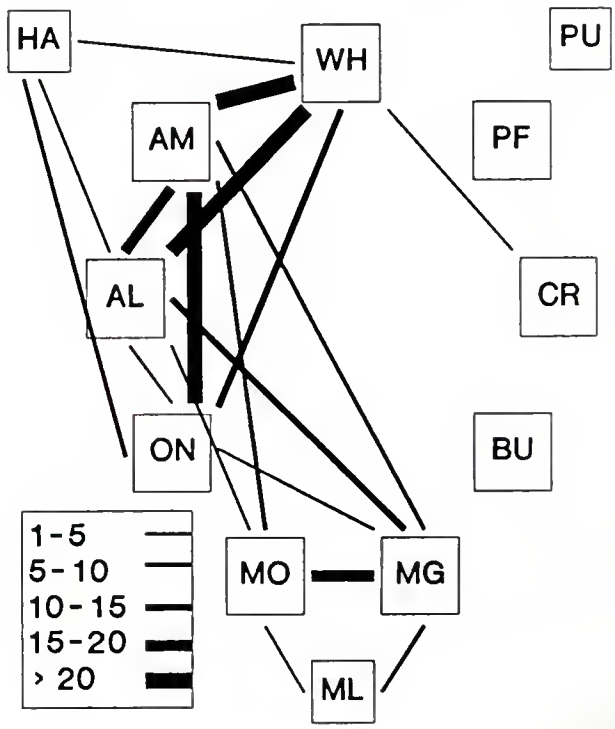
Average Session (min.)



Grooming Down Rank (min.)



Grooming Up Rank (min.)



ranking females in Main group failed to groom for more than a minute over the study and thus have no identifiable grooming relationships. Among juvenile females, one failed to form grooming relationships, one formed relationships only with closely related females, and two formed grooming relationships with unrelated or distantly related females.

I first analyzed 72 dyads to determine the effects of age, rank, and relatedness on grooming. Although the analysis is dominated by the large group (60 dyads), previous analysis has shown that large and small groups do not differ in quality of grooming, only in frequency. Within this data set there were 9 mother-daughter dyads, 4 sister dyads, 2 dyads with relatedness values of 0.25 and 4 dyads with relatedness values of 0.125. The 2 high-ranking matrilines in Main group were related and this resulted in a confounding of relatedness and rank. In order to separate the effects of rank and relatedness, I ran each analysis with all data included and then removed the 6 dyads that were distantly related and ran the analysis again. I considered an effect to be significant if it was significant in both analyses.

I used ANOVA to determine the importance of rank, relatedness, and age on 11 behaviors and ratios of grooming (Table 2.6) directly related to grooming, or correlated with grooming, to determine if sociodemographic variables affected the grooming relationships. The results showed that

Table 2.6. ANOVA results for component behaviors in grooming relationships. ANOVA considered effects of rank, age and relatedness (see text) and all 2-way interactions.

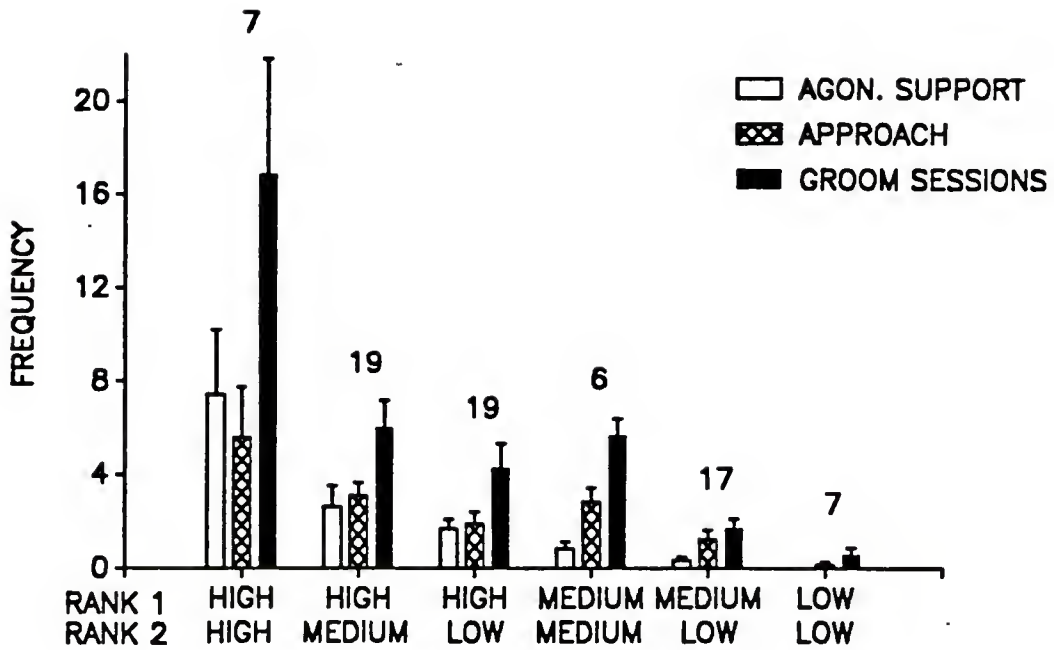
	Rank	Age	r	Rank x Age	Rank x r	Age x r
Support during aggression	0.001	NS	NS	NS	NS	NS
Approach	0.0006	0.038	NS	NS	NS	NS
Number of grooming sessions	0.0014	NS	0.0019	NS	NS	NS
Mean duration of grooming session	NS	NS	NS	NS	NS	NS
Ratio of time spent grooming by females	NS	NS	NS	NS	NS	NS
Ratio of frequency of grooming by females	NS	NS	NS	NS	NS	NS
Repsonse of female 1 to solicitation	NS	NS	NS	NS	NS	NS
Response of female 2 to solicitation	NS	NS	NS	NS	NS	NS
Rate of termination of groom by female 1	NS	NS	NS	NS	NS	NS
Frequency of unreciprocated grooming by partner 1	NS	NS	NS	NS	NS	NS
Frequency of unreciprocated grooming by partner 2	NS	NS	NS	NS	NS	NS

age, rank, and relatedness have little effect on grooming relationships except for frequency of grooming. Rank was important for support during aggression, approaches, and the number of grooming sessions. High-ranking animals approach, support and groom each other preferentially (Fig. 2.10). Frequency of grooming was positively correlated with support during aggression ($r=0.617$, $P<0.0001$) and with approach ($r=0.758$, $P<0.0001$). Support during aggression was minimal among medium- and low-ranking dyads. Age was a significant factor only for approach; adult dyads approached more frequently than adult-juvenile dyads. Closely related dyads groomed twice as frequently as unrelated dyads. It appeared that age, rank, and relatedness were not important predictors of variables that measure the quality of the grooming relationship among females. The reasons for this lack of explanatory power were explored further.

Seyfarth's Model

The model of social grooming developed by Seyfarth predicts that high-ranking animals will receive more grooming than low-ranking animals (grooming is directed up the hierarchy) and that the majority of grooming will occur between adjacently ranked females. Figures 2.7, 2.8, and 2.9 show that females groom females of lower rank more often and for longer duration than females of higher rank. A test of the amount of grooming by each member of a dyad shows that the higher-ranking female grooms significantly longer

Figure 2.10. Mean frequency of grooming sessions, support during aggression and approaches between females of different rank categories.


7
19
19
6
17
7
20
16
12
8
4
0
FREQUENCY
AGON. SUPPORT
APPROACH
GROOM SESSIONS
RANK 1
RANK 2
HIGH HIGH
HIGH MEDIUM
HIGH LOW
MEDIUM MEDIUM
MEDIUM LOW
LOW LOW

(median=0.62 minutes vs. 0.25 minutes, P=0.0047, Wilcoxon Signed Rank Test). When high-ranking animals are involved in a grooming interaction, for example, they groom an average of 4.3 minutes for every minute of grooming they receive from the lower-ranking partner. This pattern of grooming is in contrast to what has been reported for cercopithecine monkeys but consistent with results for some New World primates (Table 2.1).

I tested the second hypothesis by comparing the frequency of grooming sessions, length of grooming session, and amount of grooming by each partner as a function of occupying adjacent or more distant ranks. Animals occupying adjacent ranks did not groom more frequently (Rank Sum Test, P=0.140). Adjacent-ranked females did have longer grooming sessions (Rank Sum Test, P=0.0034) and the higher-ranking partner groomed longer (Rank Sum Test, P=0.0168) than sessions involving more distantly ranked females. This pattern is similar, in part, to results observed in cercopithecine primates and suggests a special relationship between adjacent ranked females.

Because the model does not discriminate between the effects of rank and relatedness that might account for grooming patterns among adjacent-ranked females, I made a separate comparison of related (n=10 dyads) and unrelated (n=6 dyads), adjacent-ranked females. I hypothesized that if relatedness were an important factor determining patterns of

grooming among adjacent-ranked females, then related females should groom longer and more often than unrelated females. Rates of grooming and length of grooming session did not vary as a function of rank. The frequency of grooming, however, was marginally greater for related than for unrelated females (5.9 vs. 3.3 sessions/dyad; P=0.065, Rank Sum Test). As in the general patterns of grooming discussed above, relatedness affects the frequency but not the duration of grooming among adjacently ranked females.

The results of tests of kinship are somewhat surprising because relatedness is often cited as a causal factor in social relationships of female-bonded primate groups. Figures 2.7, 2.8 and 2.9 show that closely related individuals did not consistently form grooming relationships. Of the mother-daughter dyads, 3 of 9 did not form grooming relationships and 3 more groomed less than 10 times over the course of the study. Among sibling dyads, 1 of 4 did not form grooming relationships, and none groomed more than 10 times. Strong asymmetries are evident in some grooming relationships. Female MG groomed her sister (ML) and mother (MO) 4-5 times as much as she received grooming from either. On average, daughters groomed their mothers twice as much as mothers groomed daughters, and older sisters groomed younger sisters almost 3 times as much as they received grooming.

There were no significant differences in frequency of grooming or in duration of average grooming session between mother-daughter dyads and between sibling dyads but sibling dyads sessions were more variable in length than mother-daughter ($F=4.95$, d.f.=3, 8, $P=0.031$). When sisters groomed sisters, solicitation rates and grooming rates did not differ significantly, but this may be a function of the small sample size ($n=4$). Daughters groomed mothers significantly longer than they received grooming (Wilcoxon's Signed Rank Test; $n=9$, $P=0.027$). Comparisons in which a female could groom either a mother or a sister ($n=6$) showed that daughters groomed mothers preferentially to sisters (Wilcoxon's Signed Rank Test; $n=6$, $P=0.031$). Daughters averaged 6.5 more grooming sessions with their mothers than with their sisters. Other aspects of grooming were similar however; a female groomed mother and sister at approximately the same rate, for approximately the same duration, and the sessions were approximately the same length.

Discussion

Grooming relationships in wedge-capped capuchin monkeys are differentiated by the frequency rather than the quality of grooming. These social relationships are predicated on rank and, secondarily, on relatedness. Age is an important factor in determining reciprocity of grooming. High-ranking females frequently engage in grooming sessions, are responsive to solicitation, reciprocate grooming, and are

less likely to terminate grooming. Low-ranking females do not engage in frequent grooming, are less responsive to solicitation, are less likely to reciprocate grooming, and are more likely to terminate the grooming sessions. Whereas high-ranking females initiate and maintain grooming relationships, low-ranking females withdraw from and terminate grooming. Low-ranking females do not even form grooming relationships with close kin.

A possible explanation for this pattern is that low-ranking females are peripheralized early in life and never develop affiliative relationships. Data suggest that juvenile females have a different type of grooming relationship than do adults. In this study, the 3 juvenile females that had opportunity to interact with one another did not. Interactions with adults, including mothers, often were not reciprocated or the juvenile contributed most of the grooming (Figs. 8-9). Adult females apparently do not receive the same benefits from grooming with juveniles as with other adults. A juvenile female that fails to establish grooming relationships with peers, siblings, or adults may be forced to the periphery of the group because, in the absence of affiliative relationships, social contacts will tend to be aggressive.

Because initiating grooming sessions involves approaching or maintaining close proximity to another female, grooming relationships are predicated on the

response of the target. A high-ranking female approaching a low-ranking female elicits 3 possible responses: low-ranking female moves, low-ranking female performs a submissive behavior, or low-ranking female solicits groom. All three responses can be interpreted as submissive behaviors that minimize aggression between the pair. Approach by a low-ranking female is difficult without possibility of aggressive retaliation by the higher-ranking female: as a result, low-ranking females seldom approach high-ranking females. Consequently, high-ranking juvenile females are able to initiate grooming with close relatives plus lower-ranking females whereas low-ranking juvenile females can initiate grooming only with relatives. A low-ranking female therefore, is more constrained by the social structure of status and kinship than a high-ranking female. In this study, HA has grooming relationships with 5 females, whereas ML has grooming relationships with mother and sister only and PU does not have any grooming relationships. In Splinter group, PE has a relationship with both lower-ranking females.

Although a low-ranking female cannot initiate affiliative relationships, she might respond to the initiation if grooming is important to the maintenance of a social bond. Females that move away from approaching females are withdrawing from potential grooming sessions as well as potential aggressive encounters. It is difficult for the

observer to impute motivation for moving away from an approaching female except that the impetus to move is greater than the impetus to hold one's ground and attempt to thwart aggression through an appeasement gesture. A low-ranking female may respond by inviting a grooming session. If the low-ranking female were attempting to develop relationships with high-ranking females, one would expect her to actively participate in grooming; she would respond to approaches with solicitations, reciprocating rates would be high and termination rates low. That grooming ratios and reciprocity rates are low, while termination rates are high for low ranking females, indicates that these females are tolerating grooms only as long as is necessary and are not trying to maintain grooming sessions. Low-ranking females treat grooming as an interaction to be avoided rather than encouraged. Grooming interactions may reinforce bonds among similarly ranked females, but they appear to serve more of an appeasement function between high- and low-ranking females.

Are low-ranking females peripheral? Robinson (1981) showed that low-ranking females of Main group spent more time at the edge of the group. Based on Robinson's Index of Association (Robinson 1981), females in the high-ranking matrilines have higher AI's than the females in low-ranking matrilines. Low-ranking animals have no nearest neighbors more frequently than high-ranking animals, suggesting that

they are peripheral. In Main group, low-ranking females have no nearest neighbor 40% of the time whereas high-ranking females have no nearest neighbor for 29% of observations and middle-ranking females have no nearest neighbors for 35% of observations.

Grooming as an appeasement behavior explains directional grooming down the hierarchy, but does not explain differential attractiveness of females with new infants. These interactions, however, also follow rank. Females in White and Splinter group do not show a strong infant effect, nor do they show strong rank effects (Fig. 2.5). In Main group, grooming of mothers with infants was strongly affected by rank: the high-ranking mother received twice as much grooming as the medium- and low-ranking mothers. Most of the interactions with new mothers are unreciprocated grooming sessions with higher-ranking females or kin (see O'Brien, Chapter 5). In many primate species with matrilineal dominance hierarchies, mothers with infants are the target of grooming by females attempting to gain access to the infants. Mothers with infants often withdraw from social interaction until the infant is relatively independent.

How well do the grooming data from wedge-capped capuchin monkeys fit the appeasement versus reciprocity model of social grooming? If grooming is only a form of appeasement, then low-ranking animals should receive rather

than give grooms, grooming should not be reciprocated, low-ranking females should terminate, and there should be no necessary correlation between grooming and other affiliative behaviors. Inverse correlations might be expected between aggression and grooming. The structure of grooming supports the appeasement hypothesis in general. A strong correlation exists between support during aggression and grooming, but correlations between aggression and grooming are weak and not significant. Although data from small groups are equivocal, levels of aggression among females are generally low and probability of relatedness in small groups may be high. Such patterns suggest a reduced need for appeasement. In general, White group females behave similarly to matrilineal triads in Main group, and Splinter group females behave like related versus unrelated females in Main Group.

Predictions of Seyfarth's model based on attractiveness of rank are generally not upheld. Grooming is directed down rank and low- ranking females avoid grooming rather than competing to groom. Predictions of adjacent rank are also not upheld. This is partially because it appears that daughters groom their mothers preferentially to their sisters, because daughters groom mothers less than mothers groom daughters, and because low-ranking mothers and daughters failed to form grooming relationships. There is, however, a moderately strong correlation between frequency of grooming and support during aggression which, is a

feature of models based on attractiveness of rank. This support, furthermore, is concentrated among high-ranking females that exhibit the most balanced, reciprocal grooming patterns.

It appears that grooming serves more than 1 function. The short-term benefit of grooming as appeasement serves to defuse potentially aggressive situations between females that otherwise do not have a relationship. Such females react to approaches by soliciting a groom. If a groom is given, or the female moves past, then the low-ranking female has benefitted by not being subject to aggression, and by not losing her position by supplantation. Among related and high-ranking females, grooming may serve as appeasement but it may also reinforce social bonds. That the 2 dominant matrilines in Main group were related and reciprocated grooming almost exclusively among themselves indicates that these females possessed a tolerance for each other not exhibited toward lower-ranking females. The interplay between rank, attractiveness, and relatedness is consistent with predictions; directions of grooming are contrary.

The model proposed by Seyfarth works well for ground-dwelling cercopithecine monkeys but not for species that do not exhibit strong female-dominance hierarchies, species with female dispersal, and forest species. The highly structured nature of sociality in ground-dwelling cercopithecines may result from more intense competition for

resources relative to that of forest primates (Alexander 1974; McKenna 1979). The complex grooming patterns of cercopithecines may be a refinement over the more primitive appeasement pattern exhibited by birds, and most mammals. That many Old World primates and lemurs do not exhibit directional grooming (or high levels of aggression) suggests that resource competition may not be a major factor in the development of social behavior in these species (McKenna 1979). The primitive pattern of grooming in New World primates suggests that while the social structure of 2 species appear very similar, the development of social behavior within that structure remains flexible.

CHAPTER 3

THE ROLE OF AGGRESSION IN THE SOCIAL STRUCTURE OF FEMALE WEDGE-CAPPED CAPUCHIN MONKEYS.

Introduction

The development of social structure is mediated through affiliative and aggressive behaviors among members of a group (Alexander 1974). As group living evolves, social behaviors develop to enhance the benefits of group living, regulate competition and bond group members into tolerant and even cooperating subunits. Affiliative behaviors include cooperative and altruistic acts such as allogrooming, food sharing, allomaternal care of offspring, alarm calling, and coalitionary support during aggression. Aggressive behaviors develop that maximize an individual's share of group resources at the expense of others. Social structures based on dominance hierarchies, kin relationships, or long term social contact may enhance affiliative behaviors and minimize aggression when group members recognize the organizing principles.

Aggression among group-living females is a form of social communication involved in the development and maintenance of dominance relationships (Walters and Seyfarth

1986). Aggression is often an expression of competition between individuals for food resources (Clutton-Brock and Harvey 1976) although it also is observed in nonforaging contexts (Bygott 1979; Johnson 1989). Because females maximize reproductive success through the acquisition of resources (Wrangham 1980, 1983; Janson 1984), distribution and quality of resources affect spacing patterns of females, influencing the opportunity for aggression. Fights that appear to have no motivation may in fact be used to establish social dominance between 2 individuals (Rowell 1974, Walters 1980). Recognition of a social structure may reduce the need for females to establish priority of access when resources are clumped (Alexander 1974). Supplantations, in which a female relinquishes access to a resource in response to the approach of a socially dominant female, exemplify recognition of social structure. Low-ranking females recognize the strength of dominant females and move to avoid fights.

Matrilineal relatedness and age have been implicated as organizing principles in social structures among female primates (Wilson 1975; Chapais and Schulman 1980; Trivers 1985; Chapais 1983; Walters 1986). Juveniles that are establishing social positions interact differently with other juveniles than with adults and many of these interactions involve aggression. Interactions among adults also differ from interactions among juveniles. Relatedness

among females in a group serves to mitigate aggression because closely related females have common interests (shared genes) that promote affiliation over aggression. If social dominance develops within families exhibiting low levels of aggression, it is possible to develop social structures with minimal aggression in groups of related matrilines. Few studies of aggressive interactions among females, however, have considered group differences, or sociodemographic differences within groups simultaneously.

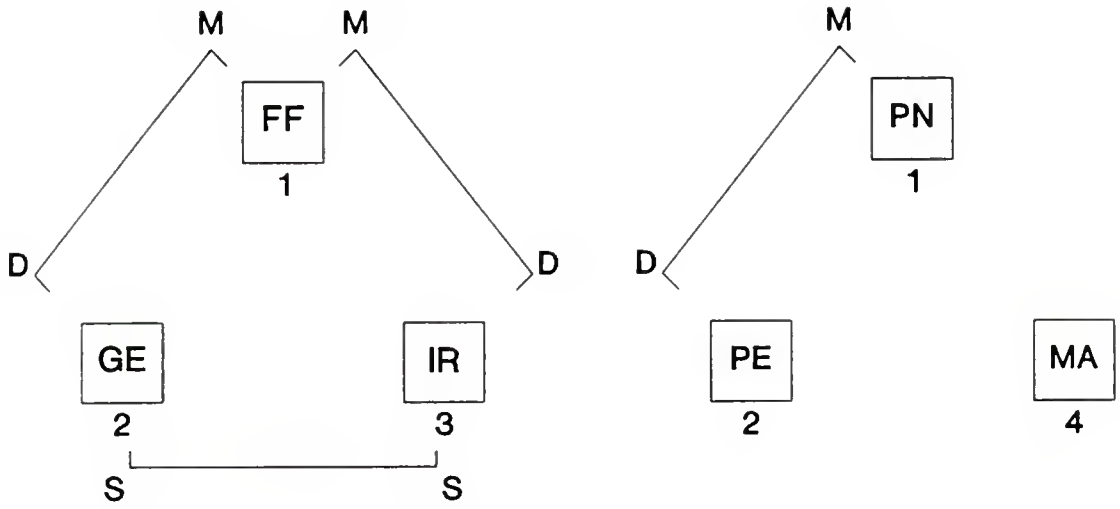
In this chapter, I examine the determinants of aggression among females in 3 groups of wedge-capped capuchin monkeys (Cebus olivaceus). I first establish that female dyads have different levels of association that are affected by group membership, social dominance, and relatedness. I then show that fights and supplantations are a function of the context in which they occur, social structure, and identities of females in the dyad. The results demonstrate that after the effects of group membership, age, rank, and relatedness of interactants are removed, a significant amount of variation is attributed to individual variability. It is argued that aggression has a social function that influences the spatial and social structure of the group, but that social structure may be of limited usefulness for predicting patterns of aggression.

Methods

I studied 7 females in 2 small groups and 12 females in 1 large group of wedge-capped capuchin monkeys (Fig. 3.1). White group had 3 females and totalled 7 to 10 individuals during the study, Splinter group had 4 females and totalled 9 to 11 individuals, and Main group ranged from 21 to 26 over the course of the study. Two females were present for only part of the study. An adult female migrated into White group during the study, but stayed for only 3 months and rarely interacted with the other females. I excluded this female from the analysis. One Main group female disappeared near the end of the study. This female was included in the analysis. Dominance hierarchies, based on direction of supplantations and winners in agonistic encounters were known for all groups (Robinson 1981, O'Brien unpubl. data). The age of each female and the matrilineal geneologies were known for all groups based on 10 years of annual censuses (Robinson 1988; Fig. 3.1). All individuals were recognizable by facial differences, and by variation in pelage, body size and habit (Robinson 1981). The 3 groups yielded 75 pairs of females (dyads) that could potentially interact.

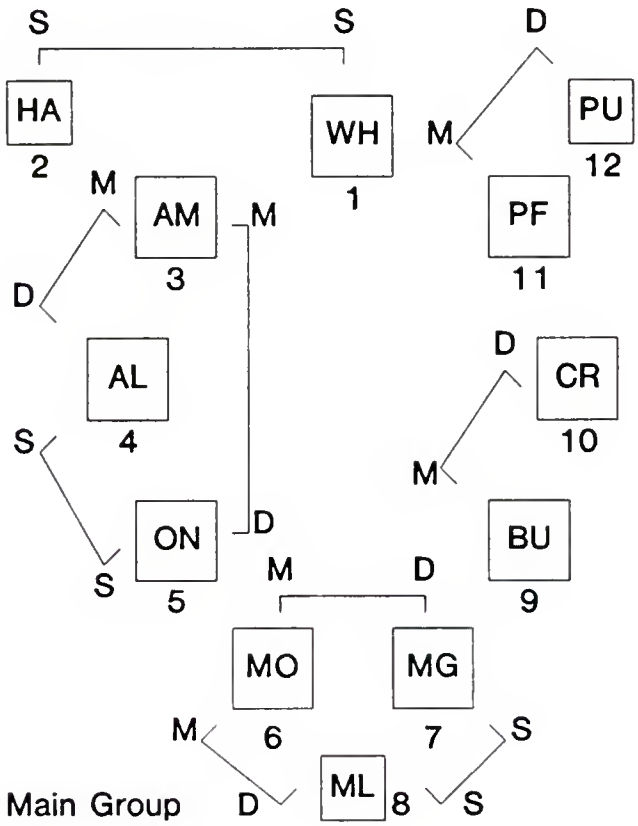
I collected data for 15 months (December 1986 to March 1988, no data collected in June 1987). Daily behavioral observations began between 0600 and 0630, and lasted for 12 hours. Observations consisted of a 20-minute focal sample on an individual female, followed by a 20-minute scan sample of

Figure 3.1. Matrilineal and dominance relationships between female wedge-capped capuchin monkeys in 3 study groups. Dominance rank is indicated below each female's identity and relatedness is indicated by brackets. M-D indicates mother-daughter relationships and S-S indicates sibling relationships.



White Group

Splinter Group



Main Group

the group and a 20-minute opportunistic sample each hour (Altmann 1974). Females were sampled systematically such that each female was included in a focal sample in each of three 4-hour time periods (morning, midday and late afternoon). During the first 12 months of sampling, I recorded all behaviors that lasted at least 3 seconds during a focal sample. For the last 3 months I recorded only social interactions that were defined as affiliative or aggressive interactions involving two or more individuals. During the scan sample, the behavior and nearest neighbor of each group member were noted.

During opportunistic samples, I recorded all observed social interactions involving females. I minimized observation bias by moving constantly through the group looking for social interactions. Because viewing conditions were excellent, I probably missed very few social interactions. There were no significant differences in the frequency of fights and supplantations between focal and opportunistic samples and I combined the data for analysis.

I analyzed 2 types of female-female aggressive social behaviors:

1. Supplantation. Female approaches or looks at another, causing other to move from an occupied position. Supplantations were completely predictable by the relative ranks of the interactants. The higher-ranking female always supplanted the lower-ranking female.

2. Fight. Female stares at, vocalizes at, lunges at, or chases other female. Occasionally grabbing or biting was observed. Response of the victim included submissive vocalization, defensive posture, or retreat.
Aggressive interactions could be ranked by level of intensity. Supplantation, threats, and vocalizations were relatively low intensity. Lunges and chases were more intense and physical contact was considered the most intense form of aggression because potential costs included injury.

Females often solicited for assistance but females were never observed to form alliances against aggressors. Females were observed forming coalitions against females (O'Brien in prep.), but presence of a coalition partner did not reverse the predicted outcome of the interaction. Females supported winners in aggression, rather than losers.

For each aggression I recorded the identities of winner and loser, the type of aggression, and, for fights, the behaviors involved. I calculated an index of aggression (AgI) for each dyad as the sum of supplantations and fights divided by the frequency of nearest-neighbor distances less than 10m. This measure adjusts the frequency of aggression to variation in proximity of individuals (Robinson 1981). Low scores result when females are tolerant of one another whereas higher scores indicate either frequent fighting or low rates of association. I analyzed the frequency of supplantation and fighting and the aggression index for each

dyad for the effects of age, rank, relatedness, group membership, and reproductive value. Age of interactant was classified as juvenile, young adult, and adult. Young adult females were at least 6 years old but were nulliparous at the start of the study. Adults were multiparous at the start of the study. No females changed age classification during the study. Dominance rank of interactants was classified as high, medium, and low. For a given dyad, female number 1 was dominant to female number 2. Matrilineal relatedness was classed as close ($r=0.5$), distant ($r=0.125$ to 0.25), and unrelated ($r<0.125$). Reproductive values for females were calculated for females in large and small groups using life tables (Robinson 1988, O'Brien unpubl. data) and standard formulae (Caughley 1976).

Nearest-Neighbor Distances

I analyzed the frequency that females were in association with other group members during all behaviors and during foraging periods to determine if females had similar opportunities to interact with group members and where differences in time spent alone occurred. Because competition for food often results in aggression within and between groups, I expected that females would spend more time alone and less time in close proximity during foraging than in general. Nearest neighbor distances estimated to the nearest meter and divided into 0-2m, 3-6m, 7-9m and 10+m classes. Distributions of close proximity (0-2m) and time

spent alone (10+m) were compared within and between groups for all behaviors and for foraging alone using 1-way ANOVAs on arcsin squareroot transformed proportions of nearest-neighbor distances in each distance class (Sokal and Rohlf 1981). The frequency of nearest neighbors for each dyad relative to the average for all other dyads was computed for an association index (AI). The index increases from 0 as a pair of females increase their frequency of association. AI was analyzed for effects of group membership, age rank and relatedness of interactants using analysis of variance.

Effects of Sociodemographic Variables

To assess the importance of different sociodemographic variables to female aggression, I used a linear model analysis of the frequency data. I chose a discrete regression model (Poisson regression) that computes parameter estimates using maximum likelihood methods (McCullough and Nelder 1983). The analysis is similar to a multidimensional contingency table analysis or log-linear model analysis. The Poisson distribution is the basic distribution for count data and Poisson regression assumes this distribution for the error term. Frequency of a behavior for a dyad was used as the dependent variable, the other behavior was used as a covariate, and sociodemographic characteristics of the interactants were used as independent variables. A separate analysis was performed for each behavior.

All sociodemographic variables that I considered, except female reproductive value, were categorical variables with discrete rather than continuous distributions. Parameter estimates for categorical variables indicate the magnitude of an effect that can be assessed for statistical significance using T-tests. Reproductive value and frequencies of other social interactions were included as continuous variables and resulting parameters were tested against the null hypothesis that the parameter was equal to 0 using T-tests.

A stepwise regression procedure was used in each analysis. First an overall mean was fit to the data and then each independent variable was added separately to the model. A variable was considered for inclusion in a model if (1) it resulted in a significant ($P<0.05$) improvement in the percent of variance accounted for by the model, (2) resulted in the smallest mean square error of variables considered, and (3) accounted for at least 5% of the total variance in the data. Variables that accounted for the most variance were sequentially included in the model. Variables were included until the addition of variables failed to satisfy criteria for inclusion. This method allowed me to evaluate the relative importance of independent variables affecting aggression based on the percent of the total variance in the data attributed to each variable. It also allowed me to compare results of regression models for each behavior to

determine if both analyses shared important variables. Shared variables indicate that an effect is an important determinant of aggression rather than fights or supplantations alone.

After the effects of independent variables in a model are accounted for, a significant amount of variability may remain in the residuals (observed error). This may indicate that one or more variables have not been considered in the model (detected as nonrandom patterns in a residual plot) or that certain dyads are interacting more or less than the model predicts (detected as outlier points on a residual plot). I identified dyads with large residuals, defined as more than 1 standard deviation (SD) above or below the mean standardized residual (Neter and Wasserman 1974), and rated them as moderate (between 1 and 2 SD) or strong (>2 SD). The residuals are used to identify dyads that were unusually aggressive or tolerant. Dyads with strong positive residuals for both behaviors are composed of individuals that have aggressive relationships (analogous to special relationships: Seyfarth 1978b; Altmann 1980; Smuts 1985). Residuals also were analyzed to determine the importance of identity of interactants to aggression after other effects were accounted for.

Results

Association Among Females

The distributions of nearest-neighbor distances for females varied considerably within and between groups (Fig. 3.2; Table 3.1). Females in White group spent less time in close proximity (1-way ANOVA; $F=4.52$, d.f.=2,16, $P=0.028$) and more time without nearest neighbors (1-way ANOVA; $F=29.82$, d.f.=2,16, $P<0.0001$) than females of Main group or Splinter group. Females spent significantly less time in close proximity when foraging than in general (paired T-test; $t=7.77$, d.f.=18, $P<0.0001$) and significantly more time without nearest neighbors (paired T-Test; $t=-4.50$, d.f.=18, $P=0.0003$). Females in Splinter group spent more time in close proximity to other group members when foraging than the other females (1-way ANOVA; $F=18.21$, d.f.=2,16, $P=0.0001$) and White group females spent more time without nearest neighbors while foraging than other females (1-way ANOVA; $F=17.02$, d.f.=2,16, $P=0.0001$). At 2-9 meter distances, there were no differences in the distribution of nearest neighbors among females.

The average AI for the 3 groups was 1.031 and there were no significant differences in AI between groups (Fig. 3.3). AI ranged from 0.53 to 1.45 in White group, 0.43 to 1.58 in Splinter group, and 0.08 to 3.38 in Main group. An ANOVA that considered the effects of dominance rank, age, and coefficient of relatedness (r) of females on AI showed

Table 3.1. Distribution of nearest neighbor distances within and between groups. Standard Deviations (SD) within each group, and within and between group variances are given. Distances are classified for all behaviors and distances during foraging only.

	Nearest Neighbor Distances, All Behaviors			
	0-2m	3-6m	7-9m	10+m
White				
Mean	0.037	0.213	0.119	0.631
SD	0.026	0.021	0.062	0.012
Splinter				
Mean	0.133	0.311	0.197	0.359
SD	0.028	0.060	0.029	0.064
Main				
Mean	0.097	0.342	0.215	0.346
SD	0.047	0.047	0.033	0.061
Variance				
Between Groups	0.0081	0.0198	0.0110	0.1004
Within Groups	0.0018	0.0022	0.0016	0.0034

	Nearest Neighbor Distances, Foraging Only			
	0-2m	>2-6m	>6-9m	>9-10+m
White				
Mean	0.000	0.265	0.109	0.626
SD	0.000	0.028	0.074	0.061
Splinter				
Mean	0.066	0.333	0.220	0.381
SD	0.017	0.049	0.088	0.041
Main				
Mean	0.009	0.289	0.271	0.431
SD	0.012	0.067	0.046	0.062
Variance				
Between Groups	0.0054	0.0045	0.0321	0.0583
Within Groups	0.0003	0.0036	0.0036	0.0034

Figure 3.2. Distribution of nearest neighbor distances for all behaviors and while foraging for each female.

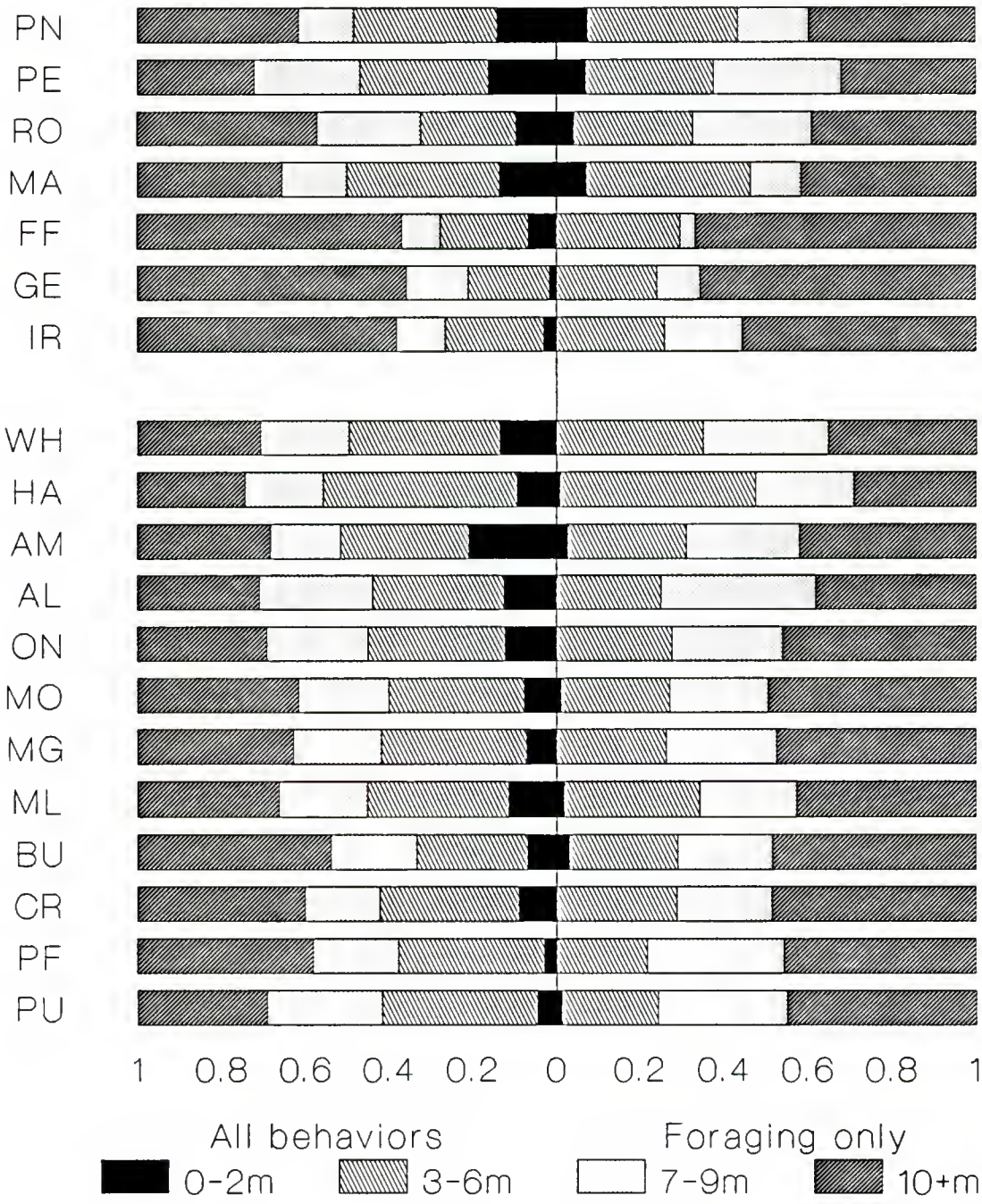
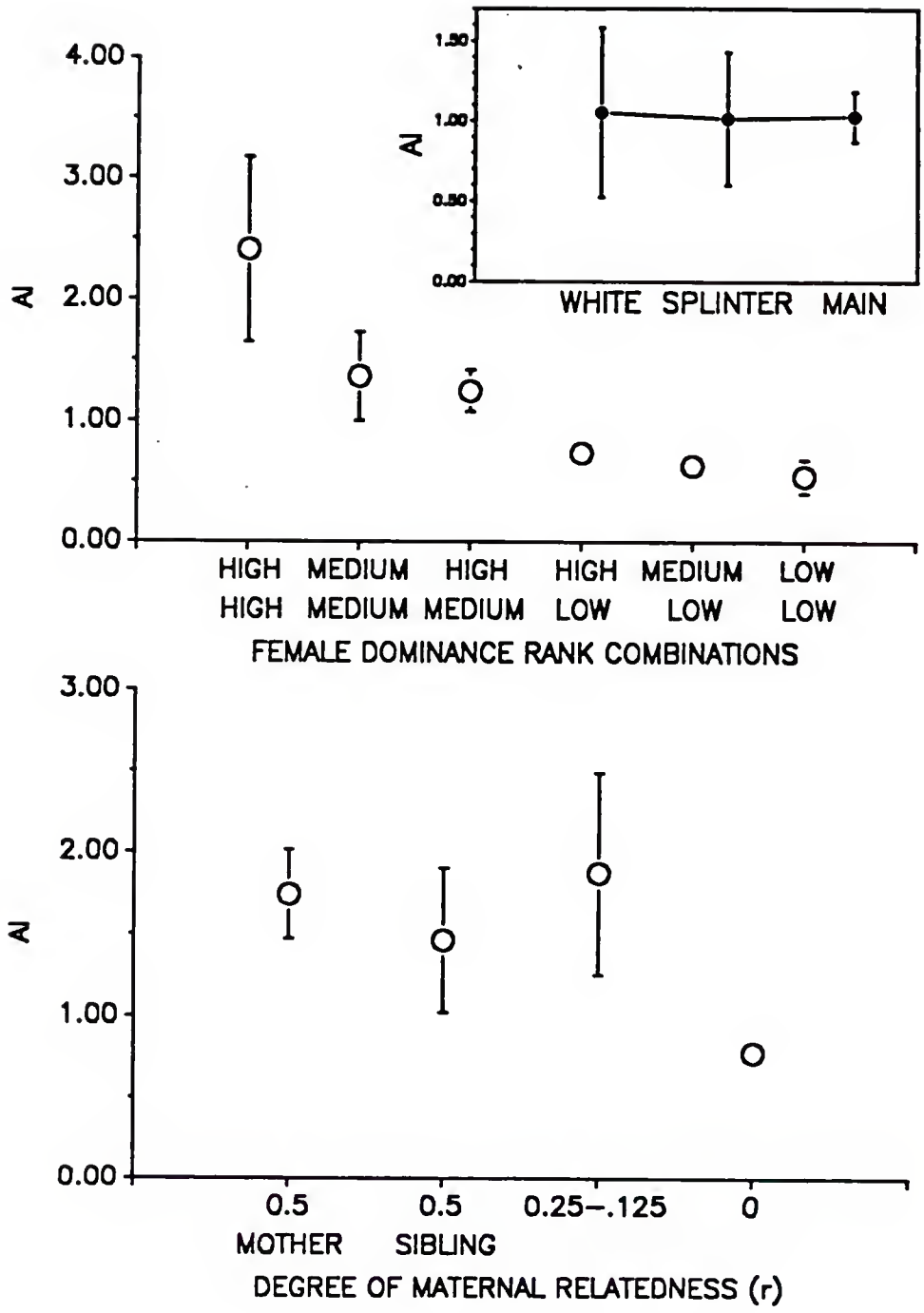

PN
PE
RO
MA
FF
GE
IR
WH
HA
AM
AL
ON
MO
MG
ML
BU
CR
PF
PU
1 0.8 0.6 0.4 0.2 0 0.2 0.4 0.6 0.8 1
All behaviors
Foraging only
0-2m
3-6m
7-9m
10+m

Figure 3.3. Distribution of Association Index (AI) among 3 groups and among rank and relatedness combinations in Main group.


AI
4.00
3.00
2.00
1.00
0.00
HIGH HIGH
MEDIUM MEDIUM
HIGH MEDIUM
HIGH LOW
MEDIUM LOW
LOW LOW
FEMALE DOMINANCE RANK COMBINATIONS
AI
1.50
1.00
0.50
0.00
WHITE SPLINTER MAIN
AI
3.00
2.00
1.00
0.00
0.5 MOTHER
0.5 SIBLING
0.25–.125
0
DEGREE OF MATERNAL RELATEDNESS (r)

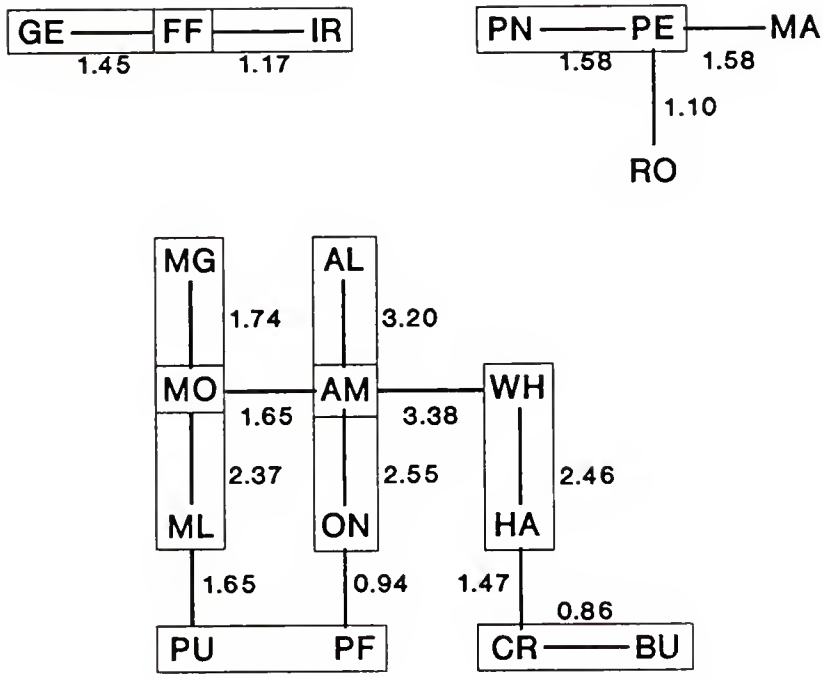
that most variation in AI was due to the dominance rank of the higher-ranking female in the dyad and to r (Table 3.2). Dyads composed of related individuals (r=0.5, AI=1.657; r=0.125-0.25, AI=1.871) associated more than dyads composed of unrelated females (r=0, AI=0.776). The top 25% of AI scores were primarily (12 of 19) among related individuals. Among closely related females, mothers and daughters associated more often than siblings (Fig. 3.3). High-ranking females associated more often than dyads in which a female was low-ranking (AI=2.409 vs. 0.663; Fig. 3.3). Associations with and between medium-ranking females were intermediate. Low-ranking females had the lowest AI values of any dyads, indicating that they were peripheral females.

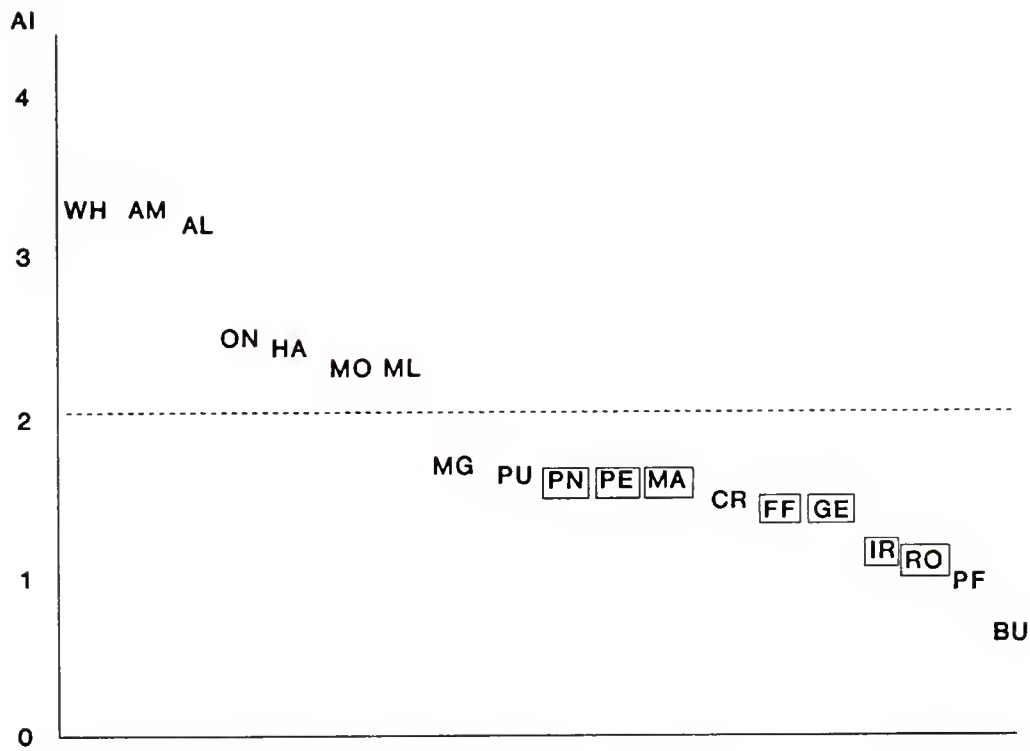
The above analysis accounted for approximately half of the variation in AI. Standardized residuals were randomly distributed (Wilks-Shapiro statistic=0.96), indicating important variables were not omitted. I attributed the residual variability in the data to individual preference among females. A maximum spanning tree analysis (MST; Morgan et al. 1974; Fig. 3.4) using AI values shows which females are closely linked. In White group, The mother (FF) is the focal female in the group. In Splinter group, the juvenile female (PE) was closely linked to the other adult females but the adults were not closely associated with one another. In Main group closely associated females were related and/or high-ranking. Only females of the lowest-ranking matriline

Table 3.2. Main effects ANOVA for AI. Mean squares are calculated and tested using Type III sums of squares. The number after each variable identifies characteristics of female 1 and female 2. The first female is higher ranking.

Model	d.f.	Mean Square	F	P>F
Rank 1	2	1.115	4.425	0.016
Rank 2	2	0.352	1.397	0.254
Age 1	2	0.556	2.206	0.116
Age 2	2	0.201	0.798	0.458
r	2	1.236	4.905	0.010
Error	64	0.252		

Figure 3.4. Maximum Association Index (AI) scores among pairs of females in 3 groups. a) Maximum spanning tree for AI scores. Boxes indicate relatedness of r=0.5. b) Ranked maximum AI scores for all females in study. Females in boxes are from small groups. AI=2.1 is used as middle reference line; scores greater than 2.1 indicate at least 1 close association.


GE
FF
IR
1.45
1.17
PN
PE
MA
1.58
1.58
1.10
RO
MG
AL
1.74
3.20
MO
AM
WH
1.65
3.38
2.37
2.55
2.46
ML
ON
HA
1.65
0.94
1.47
0.86
PU
PF
CR
BU


AI
4
3
2
1
0
WH
AM
AL
ON
HA
MO
ML
MG
PU
PN
PE
MA
CR
FF
GE
IR
RO
PF
BU

were not connected. Patterns of dominance rank and relatedness were not predictable when juvenile females were considered. Juveniles associated often among themselves (ML-PU=1.65, HA-ML=1.74) and HA associated with lower-ranking adults (CR and MG).

I next ranked females by their maximum AI scores to show that group membership and dominance rank affected AI values among females (Fig. 3.4). High- and middle-ranking females in Main group form at least 1 close association (AI>2.0), whereas low-ranking females of Main group and all small-group females did not form close associations among themselves. That small-group females exhibit AI patterns characteristic of low-ranking females, irrespective of their own rank and relatedness patterns, confounds generalizations concerning rank and relatedness. Perhaps these factors are meaningful only as group size increases.

Aggression Among Females

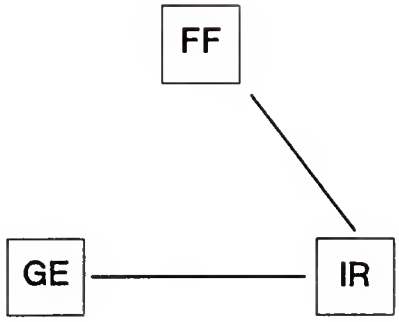
I observed 222 fights and 186 supplantations among females. Main-group females were more aggressive, per dyad, than small-group females (Fig. 3.5; Table 3.3). In small groups, supplantations were more common than fights, and foraging was the most common context for aggression. Females in small groups also had much lower Aggression Index (AgI) scores than females of Main group (Fig. 3.6), suggesting greater tolerance for one another. Among Main group females, in contrast, fights were more common than supplantations and

Table 3.3. Involvement in fights and supplantation during foraging for a subset of data in which context was identified for each female. Data are presented by % for aggressive interactions won by each female and total involvement. Sample sizes are given in parentheses.

	Wins		Total	
Female	Fight	Supplantation	Fight	Supplantation
WH	50 (24)	39 (36)	50 (24)	39 (36)
HA	56 (9)	50 (10)	56 (9)	50 (10)
AM	36 (11)	50 (12)	31 (13)	43 (14)
AL	0 (7)	86 (14)	8 (13)	56 (26)
ON	18 (17)	57 (7)	23 (22)	47 (17)
MO	33 (3)	0 (0)	43 (14)	70 (10)
MG	0 (1)	0 (0)	19 (16)	71 (14)
ML	100 (1)	0 (0)	20 (10)	60 (10)
BU	100 (2)	0 (0)	67 (3)	75 (4)
CR	100 (3)	100 (1)	80 (10)	62 (8)
PF	0 (0)	0 (0)	0 (2)	0 (2)
PU	0 (0)	0 (0)	65 (17)	38 (8)
PN	100 (1)	100 (3)	100 (1)	100 (3)
PE	0 (0)	100 (1)	0 (0)	100 (2)
RO	0 (0)	0 (0)	0 (1)	0 (3)
MA	0 (0)	0 (0)	0 (0)	0 (0)
FF	0 (0)	0 (0)	0 (0)	100 (1)
GE	100 (1)	0 (0)	100 (1)	0 (0)
IR	0 (0)	0 (0)	100 (1)	100 (1)

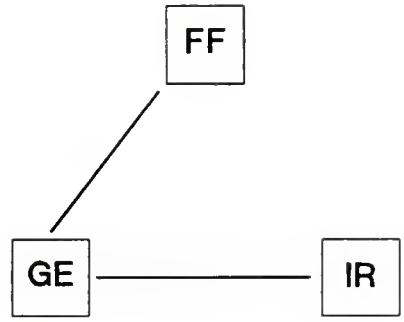
Figure 3.5. Distribution of aggression for a) 2 small groups and b) 1 large group of wedge-capped capuchin monkeys.

Supplantation



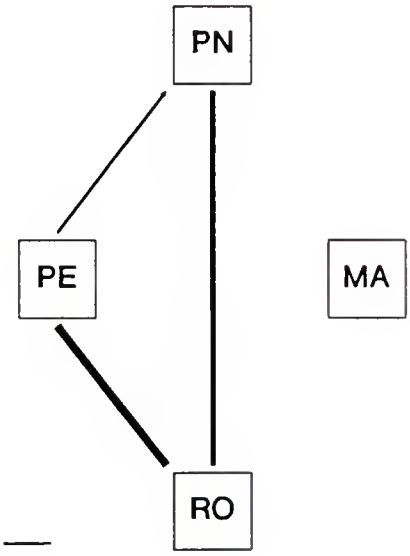
1—

Aggression



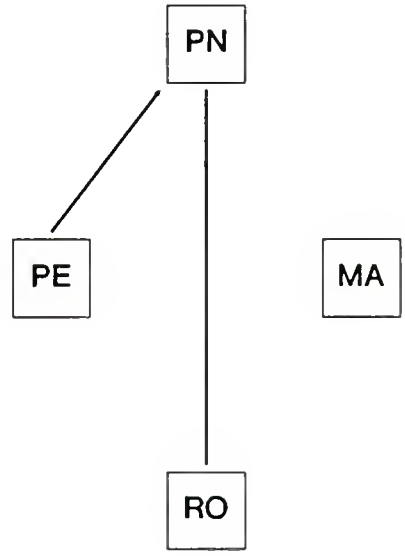
1 - 2 —

Supplantation



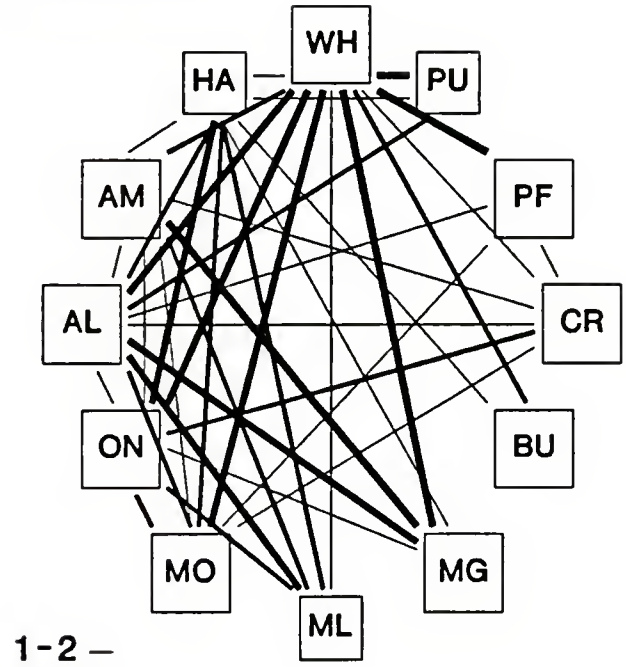
1 - 2 —
3 - 4 —
5 - 6 ▬

Aggression



1 - 2 —

Supplantation



1-2 —
3-4 —
5+ —

Fight

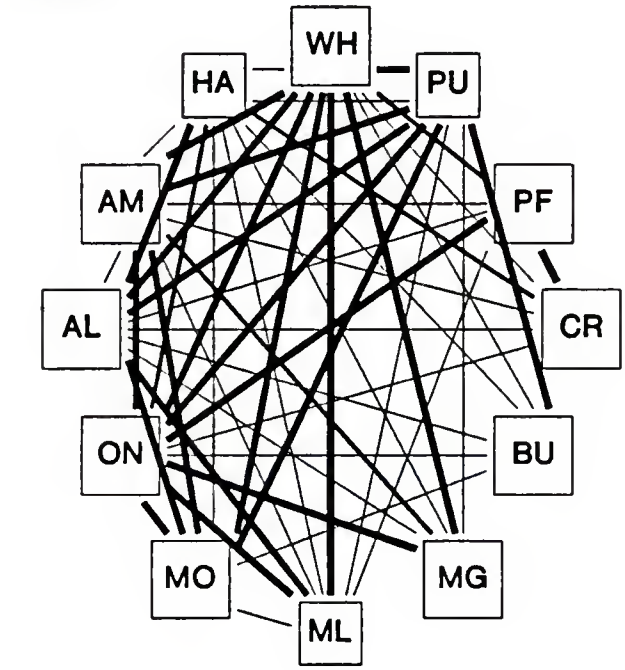
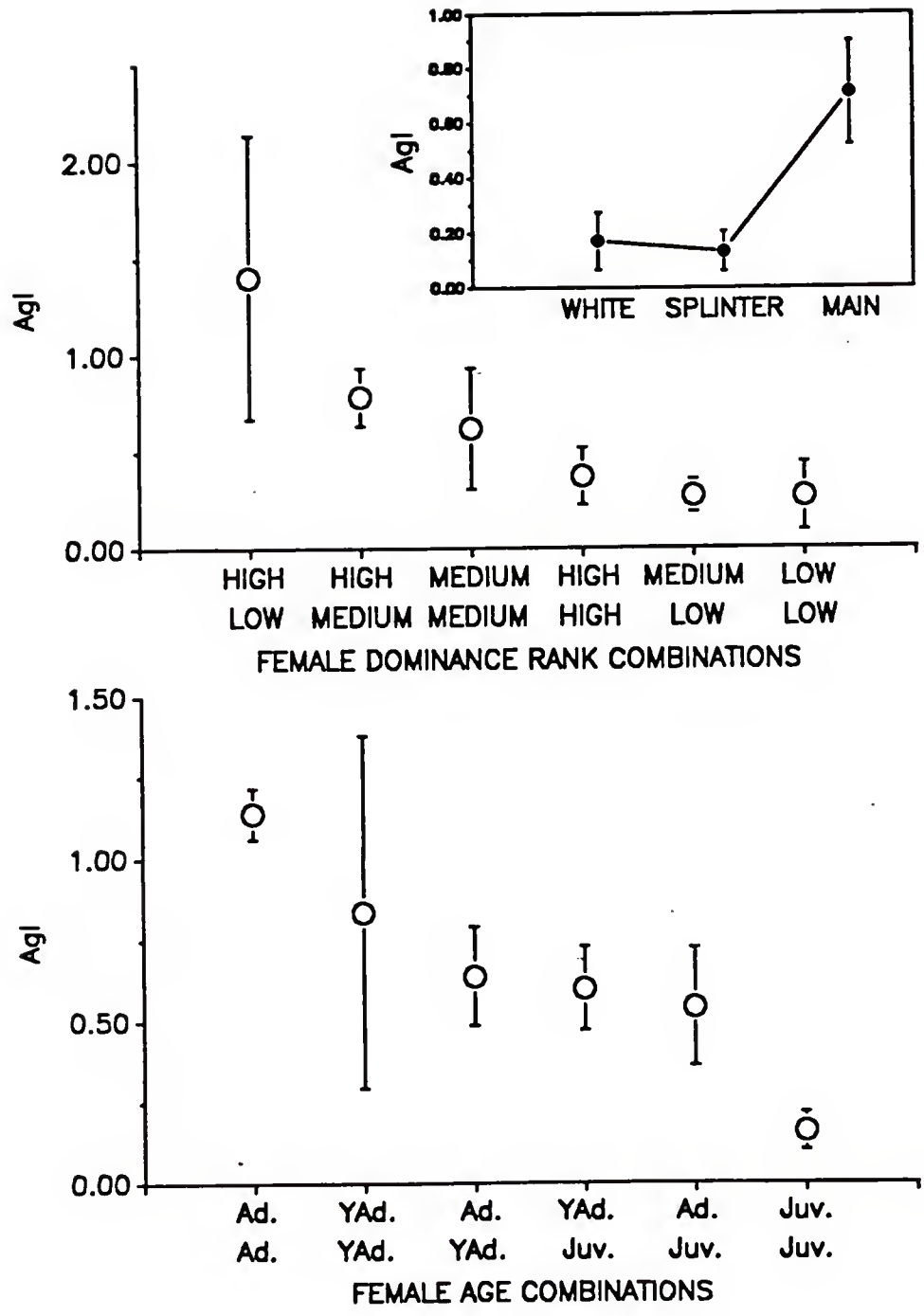


Figure 3.5 -- continued

Figure 3.6. Distribution of Aggression Index (AgI) among 3 groups and among rank and age combinations of Main group.


AgI
2.00
1.00
0.00
HIGH LOW
HIGH MEDIUM
MEDIUM MEDIUM
HIGH HIGH
MEDIUM LOW
LOW LOW
FEMALE DOMINANCE RANK COMBINATIONS
AgI
WHITE
SPLINTER
MAIN
1.50
1.00
0.50
0.00
Ad. Ad.
YAd. YAd.
Ad. YAd.
YAd. Juv.
Ad. Juv.
Juv. Juv.
FEMALE AGE COMBINATIONS

dominance-rank effects were apparent. Females with the highest AI values (high-ranking females primarily) were more often involved in supplantations than were other females. Patterns of fighting were more diffuse. The 5 highest-ranking females initiated 87% of fights and 99% of supplantations for which contexts were identified. Fights occurred more often in a nonforaging context (mean during foraging 38.5%, SE= 7.34, $P<0.001$) whereas supplantations occurred equally often during foraging and other contexts (mean during foraging= 50.9%, SE=5.88). The highest-ranking females were as likely to fight during foraging as at other times, but the lowest-ranking females were involved in fights primarily during foraging. The intermediate females were involved in fights more often during a nonforaging context. High-ranking females were involved in supplantations slightly more often during nonforaging periods, but other females were involved in supplantations primarily during the foraging context. Although most supplantations occurred among high-ranking and high-medium-ranking dyads (4.0 and 4.4 per dyad respectively), most fights occurred among high-medium- and medium-ranking dyads (4.9 and 5.5 per dyad respectively). Low-ranking females were involved in fights 1.6 times as often as in supplantations, medium-ranking females 1.4 times and high-ranking females 1.1 times.

Because fights and supplantations were so rare in small groups, I only analyzed Main-group females to assess the relative importance of sociodemographic variables affecting aggression. Poisson regression analysis (Table 3.4) showed that the rank of female 1 (the higher-ranking female of the dyad) explained most of the variability in supplantations (35.2%); high-ranking females were more than twice as likely to supplant other females as middle- or low-ranking females. Dyads that fought frequently also were more likely to be involved in supplantations. The correlation between fighting and supplantation was especially pronounced for dyads involving high-ranking females (r_s=0.55, P<0.0001). Finally, young-adult females were much more likely to be supplanted than other age classes (5.0 vs. 2.3 per dyad). This was true even for the high-ranking young-adult female.

A Poisson regression analysis of fights among females (Table 3.4) indicated that the dominance rank of female 2 accounted for most of the variability in the data (20.2%). Middle- and high-ranking females were involved in fights more than low-ranking females. Age of female 1 also was important; adult and young-adult females were involved in fights more often than the juvenile female. The correlation between fighting and supplantation accounted for an additional 5.2% of variation.

An analysis of variance of sociodemographic effects and the association index on AgI values for Main group indicated

Table 3.4. Analysis of Deviance for Poisson regression of sociodemographic variables on frequency of coalitions, aggression, and supplantation among female capuchin monkeys in a large group. The number after each variable identifies the first or second female of the dyad. First female is higher ranking than second female. Percent variance is the amount of variation accounted for by a given variable.

Model	d.f.	Deviance Difference	$P>X^2$	% Variance
<u>Supplantation</u>				
Agonistic	1	17.3	0.0001	10.5
Rank 1	2	50.4	0.0001	35.2
Age 2	2	11.4	0.003	5.5
Residual	59	101.6	0.0001	
<u>Agonistic</u>				
Supplantation	1	12.9	0.0001	5.2
Rank 2	2	22.8	0.0001	20.2
Age 1	2	16.0	0.0001	7.2
Residual	59	168.6	0.0001	

no significant effects. This was because certain classes of individuals had such high variance in interactions that differences were obscured. High-ranked females were most aggressive toward low- and middle-ranking females but were tolerant of other high-ranked females (Fig. 3.6). Low-ranked females had both the lowest and highest AgI scores as well as the highest variability in aggression. The patterns of AgI for age combinations also were inconsistent. Adults and young-adults were most aggressive toward females in their respective age classes but there was exceptionally high variance among young-adult females. Juvenile dyads have the lowest AgI scores indicating these females are very tolerant toward one another.

The relationship between AI and AgI was not significant for Main group. As AgI scores increase, however, AI tends to decrease. Among the top 25% of AgI scores, AgI and AI were negatively correlated (r_s=0.565, P=0.012). Only 1 dyad (WH-ON) was ranked both in the top 25% of AI scores and the top 25% of AgI scores, indicating close association with high aggression. Because many females were rarely aggressive toward one another, AgI scores less than 0.8 were not correlated with AI. For AgI values greater than 0.8, AI is uniformly low.

Individual Variability in Aggression

Because the analyses of Main group showed significant residual variation in aggressive behaviors, I examined

residuals of supplantations and fights to identify additional sources of variation. Standardized residuals for supplantation and fights were randomly distributed except for a few obvious outliers in the supplantation data (Wilks-Shapiro statistic = 0.87 for supplantation, 0.92 for fights) suggesting that no important variables were omitted. An examination of the distribution of large residuals ($X \pm 1$ SD) showed that dyads involving high- or medium-ranked females had the poorest fit: medium-ranked females were involved in more aggression than expected but high-ranking females were as likely to be overestimated as underestimated. Among age classes, dyads with young-adult females tended to be more aggressive than expected by the regression and dyads containing adult females were as likely to be more aggressive as less aggressive.

Analysis of variance of the standardized residuals for supplantations and fights showed that identity of the interactants accounted for an additional 38% and 46% of residual variation respectively (Table 3.5). The identity of female 2 was significant in both analyses. In supplantations, one female (ON) was a victim significantly more than expected whereas another (HA) was a victim significantly less than expected. During fights, 2 females (WH and ON) were aggressors significantly more than expected. Two female (MO and PU) were victims significantly more than other middle and low ranking females. This

Table 3.5. Main effects ANOVA examining the effects of female identity as aggressor and victim on supplantation and fights after the effects of covariation between behaviors, age and rank have been removed. Dependent variables are the standardized residuals from the Poisson regression and independent variables are female identities in Main group. All F-tests use Type III mean square.

Model	d.f.	Mean Square	F	P>F
<u>Supplantation</u>				
Aggressor	10	1.48	0.832	0.399
Victim	10	3.72	2.092	0.045
Error	45	1.78		
Total	65			
<u>Fights</u>				
Aggressor	10	3.85	1.812	0.086
Victim	10	4.82	2.269	0.030
Error	45	1.78		
Total	65			

analysis suggests that individual differences are of major consequence after age, dominance rank, and relatedness are considered. The tolerance between 2 females, or lack thereof, has a component of individual preferences that limits prediction of aggressive interactions based solely on social structure.

Discussion

Group size and social structure of wedge-capped capuchin monkeys influence the amount of aggression that a female experiences. Females vary in their use of aggression and in their participation in aggression in a number of ways. High-ranking females use aggression to establish or maintain social dominance and access to resources. Small group females and low ranking females in large groups generally do not use aggression. Individual differences among females in the large group were greater than variation due to the age, dominance rank, and relatedness of interactants. The results indicate that while social structure provides a mechanism for reducing the costs of aggression associated with group living, variance in aggression among females remains primarily a function of the individuals involved, their history of interaction, and the context in which aggression occurs.

Patterns of aggression varied in a foraging versus a nonforaging context, indicating that females use aggression differently when competition concerns food or assertion of

rank. Rowell (1974) and Walters (1980) report the use of unprovoked aggression to establish or assert dominance rank over another individual. Although fights and threats have potential costs for both parties, there is little risk of escalation among females unless a resource is at stake. Fights in a nonforaging context (social fights) can be used to develop or maintain the rank relationships among females with minimal costs. Familiarity with the competitive abilities of other females reduces the need for repeated testing of dominance (Johnson 1989) and may reduce the need for fighting during foraging. A low-ranking female can respond to the approach of a higher-ranking female by relinquishing the food or foraging site if the resource is not worth defending. Thus supplantation replaces fighting in a situation where risk of escalation increases as the value of the resource increases.

Spacing patterns showed that certain females were gregarious and others solitary. In the large group, the 4 highest-ranking adult females had average AI values over twice as high as the 5 lower-ranking adult females. The females that avoided association rarely initiated aggressive interactions and were rarely involved in social fights. Spatial relationships therefore reflected a female's competitive abilities in the large group: females that failed to win aggressive interactions withdrew to the edge of the group and avoided interacting with other group

members. Peripheral females became involved in aggression primarily during foraging, when resource distribution forced them into proximity of other females. The most common aggressive interaction was supplantation, supporting the idea that familiarity reduces the need for more vigorous aggression.

The development of aggression and association patterns begins when juvenile females attempt to integrate into the social network of the group and may persist into adulthood (Hausfater et al. 1982; Cheney 1977). Juvenile females associated with many adult females and amounts of aggression received increased as a juvenile's dominance rank declined. Juvenile females initiated more grooming sessions with adults (see O'Brien, Chapter 2) but their grooming often was not reciprocated. Juveniles apparently used association to develop relationships with adults. The response of the adults varied with dominance rank: higher-ranking females often were aggressive and lower-ranking adults avoided higher-ranking juveniles or were supplanted during the juvenile's approach. The predicted outcome of adult responses to juvenile social overtures was that lower-ranking juvenile females would fail to establish social relationships and higher-ranking juveniles would establish their social dominance over adult females.

Dominance and other social relationships developed as juveniles often persist into adulthood. Several adult

females involved in the present study exhibited association, affiliation, and aggression patterns that are similar to those exhibited as juveniles (O'Brien and Robinson 1990). Hausfater et al. (1982) reached a similar conclusion concerning dominance relationships of female yellow baboons. Such relationships are not always stable, however, and affiliations may change as group composition changes through maturation of juveniles and death of older animals (Altmann and Altmann 1979). As potential partners change, histories of aggression between individuals and dominance relationships may become more important to the social network. Affiliative peer relationships among juveniles may change as higher-ranking females become active in the adult social network and the lower-ranking females become increasingly peripheral. Competition for social partners may change dramatically when a group member dies (O'Brien unpubl. data, Chapter 2; Wilson 1975; Altmann and Altmann 1979).

The importance of demographic factors is highlighted by differences in patterns of aggression among females in large and small groups. Large-group females were in association with other females more often than females in small groups and the opportunity for aggression increased as a result. Social fighting was common in the large group and never occurred in the small groups. Females in small groups behaved like low-ranking females of large groups. There are

2 plausible reasons for this result. First, small groups, such as Splinter group, formed from fissioning of low-ranking matrilines from a large group (Robinson 1988; Dittus 1988 for Macaca sinica). If this is a common pattern for small-group establishment, then small-group females would, in fact, be low-ranking large-group females. Second, within group competition for resources is less in small groups than in large groups (Srikosamatara 1987). Because of the low number of females involved and wide spatial distribution foraging, small-group females did not need to frequently exert dominance over one another, unless the resource was very patchy. Social fighting may be rare among females that do not experience strong feeding competition. The most common food resources from which females were supplanted were trees with few foraging position available. The palm Copernicia tectorum which is too small for females to share unless they are extremely tolerant of one another, and the small-crowned Guazuma tomentosa, were sites of frequent supplantations (Robinson 1986; O'Brien unpubl. data).

Individual identity of the aggressor and the victim explained 38% and 46 % of the variability in supplantations and aggressions after important social and demographic variability was removed. Variation among individuals in Main group was considerably larger than variation due to age, rank, or relatedness. Strong individual variation should be expected among long-lived social primates: patterns of

association and aggression reflect the general social structure of the group but also reflect the checkered history of interactions between group members (de Waal 1982; O'Brien and Robinson 1990).

Because the social structure must be learned and reinforced, the interactions that occur within a social framework will not always be predictable. Females do not sort into discrete behavioral classes as a function of social structure. Age, rank, and matrilineal affiliation may be sufficient to identify individuals in most groups, but they may not be sufficient to determine the social network. Individual variation in aggressiveness, for example, affects the likelihood of social relationships developing between high- and low-ranking females. In Main group, each high-ranking female is most aggressive toward a different set of lower-ranking females. Levels of aggression by high-ranking females are not predictable by rank or by matriline. Sisters exhibit very different levels of aggression. The amount of aggression received by a female resulted from an interaction of dominance rank, age, foraging context, and spatial position in a group. A low-ranking juvenile might receive more social aggression than would her mother, whereas both might receive similar amounts of aggression during foraging.

Demographic considerations such as number of females in a group and their distribution into various matrilines and age classes affect aggression (Chivers 1974; Altmann and

Altmann 1979; Dunbar and Dunbar 1976). The absence of juvenile peers may increase rates of juvenile-adult interactions (Walters 1986). If the juvenile is higher-ranking, the interactions may consist mostly of supplantations and affiliative behaviors. If the juvenile is lower-ranking, the interactions may consist of aggressive interactions and no affiliative behaviors. The presence of an infants might mediate aggressive relationships between the juveniles and adults if mothers require allomaternal care for the infants. A small group of related females might interact less than a large group because of less need to reinforce social dominance within a matriline. As group size increases, the need to establish and maintain a social position with unrelated females increases the rate of social fighting. Perhaps social relationships are best viewed as a facultative response to the amount and type of interaction required to enforce the social structure for a group of a given size and composition. An individual's social strategy would then depend on group composition, group relatedness, and her own position within the group's dominance hierarchy.

These results underscore the importance of individual response to variation in number and kinds of females with whom an individual must interact. Aggression is a cost of group living and this cost is not equally distributed among females within groups or among females in different groups. Within groups, competition for resources and social

relationships among females are mediated, in part, through aggression, through social structure, and through individual recognition of that structure.

CHAPTER 4

FEMALE-MALE SOCIAL INTERACTIONS IN WEDGE-CAPPED CAPUCHIN MONKEYS: BENEFITS AND COSTS OF GROUP LIVING.

Introduction

Social interactions between the sexes present an especially interesting example of tradeoffs between cooperation and conflict for group-living species (Crook 1970; Walters and Seyfarth 1986). For many primate species, females maximize reproductive success through food acquisition (Wrangham 1980, 1983; Janson 1984), whereas males maximize reproductive fitness through mate acquisition. Resource distribution may determine how females space themselves in the environment to maximize resource acquisition and how males space themselves in order to maximize access to females. Male and female reproductive strategies are complementary when males participate in defense of females or enhance access to resources but are antagonistic when males interfere with female food acquisition or harass females. A prudent social strategy for a female that interacts with males should emphasize contact with males that provide benefits for her or her offspring

and avoidance or intolerance of males that do not provide benefits (Robinson 1983).

Examples of affiliative female-male interactions include sexual consorting (Seyfarth 1978a, b; Rasmussen 1980; Smuts 1985, 1986), special relationships (Altmann 1980; Smuts 1985), and alloparental care by males (Brown and Mack 1978; Fossey 1983; Terborgh and Goldizen 1985). Examples of avoidance include sex-specific partitioning of space during foraging (Robinson 1981, 1986), females refusing sexual advances of males (Smuts 1986), and female aggression toward males (Hrdy 1977; Cheney 1981; Robinson 1981).

Although male-female social relationships are usually defined by sexual relationships (or lack thereof), the consequences of these relationships extend to all aspects of the female's behavior toward a given male. The social relationship between two individuals should reflect the balance between the benefits that the individuals provide each other, and the costs they impose on each other. Males that provide benefits to females are expected to have a strong affiliative component to the social interactions with females, whereas males that provide minimal benefits should have correspondingly weak affiliative interactions. These assumptions are a logical extension of reciprocal altruism theory (Trivers 1971; Bertram 1982): that natural selection will favor individuals who help those that help in return

because, over time, participants obtain benefits that outweigh the costs of the interactions.

What benefits might a male offer to a female (or females)? Males that participate in group defense against predators or in intergroup competition for resources contribute indirectly toward individual female reproductive success by decreasing probability of mortality through predation or increasing female access to resources (Wrangham 1980; van Schaik 1983). Individual males may offer superior genes that promote the survival of offspring, provide parental care that benefits both the female and the offspring, allow a female access to resources thereby reducing intragroup competition, or provide a female with support during agonistic interactions with other group members (Seyfarth 1978b; Robinson 1982). The ability of a male to provide all or some combination of benefits will influence a female's willingness to maintain an affiliative relationship with that male. While direct measurement of potential benefits of males is difficult, analysis of female social relationships with males may reveal which males are considered as beneficial by females. Knowledge of the ability of these males to provide benefits may then reveal why certain males are preferred.

Wedge-capped capuchin monkeys (Cebus olivaceus) are ideal subjects for testing theories of social behavior and group living. The groups are female bonded, range in size

from 5 to 40+, and have a number of matrilines within groups. Groups usually have 1 breeding male, with several subadult and juvenile males that are either born in or immigrate into the group. Males have a size-based dominance hierarchy and females have a stable matrilineal dominance hierarchy. Wedge-capped capuchin monkeys are highly social; aggressive and affiliative interactions are easily quantified. They spend most of the day within 20m of the ground and observation conditions are excellent. Previous work has shown the benefits of group living in relation to access to resources, reduced vigilance for predators, and reproductive success for males and females (Robinson 1981, 1986, 1988a, b; Srikosamatara 1987, de Ruiter 1986).

This study investigates how female capuchin monkeys socially mediate their relationships with males so that the benefits offered by males are maximized and the costs of males are minimized. First I examine the spatial proximity patterns of males and females to determine if females come into contact with males at the same rate as with females. Proximity patterns should be similar among females and between males and females if the cost of contact is similar for the two sexes. Next, I analyze the distribution of social interactions between males and females to determine how interactions with males differ from interactions with females. Finally, I determine what sociodemographic characteristics influence social interactions between the

sexes and how these characteristics may relate to costs and benefits of males to females.

Methods

I studied 8 females in 2 small groups and 12 females in 1 large group of wedge-capped capuchin monkeys. White group ranged from 7 to 10, Splinter group ranged from 9 to 11, and Main group ranged from 21 to 26 individuals over the course of the study. Dominance hierarchies and matrilineal relationships among females were known for all groups and all individuals were recognizable by facial differences, and by variation in pelage, body size, and habit (Robinson 1981, 1988a). Females and males less than 2 years old at the start of the study were excluded from this analysis. Male composition of groups varied: 4 White group females interacted with 1 adult male at a time during the course of the study (3 different males in total), 4 Splinter group females interacted with 1 adult and 1 subadult male, and 12 Main group females interacted with 1 adult and 6 subadult males. One subadult male of Main group became the dominant adult male during the study. The 3 groups yielded 96 female-male dyads that could potentially interact.

I collected data for 15 months (December 1986 to March 1988). Daily behavioral observations began between 0600 and 0630, and lasted for 12 hours. Observations consisted of a 20-minute focal sample on an individual female, followed by a 20-minute scan sample of the group and a 20-minute

opportunistic sample each hour (Altmann 1974). Females were sampled systematically such that each female was included in a focal sample in each of three 4-hour time periods (morning, midday and late afternoon). During the first 12 months of sampling, I recorded all behaviors that lasted at least 3 seconds during a focal sample. For the last 3 months I recorded only social interactions that were defined as affiliative or agonistic interactions involving two or more individuals. During the scan sample, the behavior and nearest neighbor of each group member were noted.

During opportunistic samples, I recorded all observed social interactions involving females. I minimized observation bias by moving constantly through the group looking for social interactions. Because viewing conditions were excellent and social interactions were often accompanied by vocalizations (aggression, grooming of dominant male), I probably missed very few social interactions. I tested the distribution of social behaviors in focal and opportunistic samples (using G-test; Sokal and Rohlf 1981) and found that the only difference between the data sets was in the frequency of supplantations. Supplantations were rarely recorded in opportunistic samples because they are subtle behaviors of short duration. Because the data sets were comparable, I combined data from focal and opportunistic samples for analysis of frequency of

behaviors. I used nearest neighbor distances from scan samples for the analysis of spatial proximity.

I analyzed 4 types of female-male social behaviors:

1. Supplantation. Individual approaches or looks at another causing other to move from an occupied position. I observed only female supplantation by males but male supplantation by females is known to occur.

2. Male aggression or female defensive. Male lunges at, stares at, vocalizes at, or chases female. Female responses include submissive vocalization, defensive posture, retreat, or retaliatory aggression.

3. Female aggression. Female lunges at, stares at, vocalizes at, or chases male, often supported by other females. Male responses include submissive vocalization, defensive posture, retreat, retaliatory aggression, or ignoring female(s).

4. Grooming session. Grooming involves examining fur and skin, removing items of dirt and ectoparasites with teeth and hands. Grooming sessions vary in duration, number of grooms involved, and reciprocity between interactants. Males rarely reciprocate the grooming they receive.

For each behavior I recorded the identities of interactants and the frequency of a behavior between a dyad. I analyzed the frequency of interaction for each behavior for the effects of female age, female reproductive value, female rank, degree of relatedness between interactants,

male age, male rank, male immigration status (resident versus immigrant) and group membership. These variables are called sociodemographic variables. Other social interactions were included in the analysis as covariates to determine if occurrence of one behavior affected another behavior.

Nearest-Neighbor Distances

I analyzed the frequency that females were in association with other females or males to determine if females had similar opportunities to interact with each sex. Nearest-neighbor distances were divided into 0-1m, 1-2m and >2m. The 2 distributions were then tested for goodness-of-fit (using G-tests; Sokal and Rohlf 1981) against a random distribution of expected nearest-neighbor distances weighted by the number of female-female and female-male dyads.

Distributions of Interactions

The frequency with which females interacted with females and with males was examined to determine if interactions were affected by the number of potential interactants or by spatial proximity to either sex. Frequencies of supplantation, male aggression, female aggression, and grooming sessions were determined for all female-female and female-male dyads. The distribution of behaviors between females and males was tested for goodness-of-fit (G-test) against a random distribution of expected frequencies weighted by the number of female-female and female-male dyads. The observed distribution also was tested

against a random distribution weighted by the frequency that males and females were observed as nearest neighbors.

Effects of sociodemographic variables

To assess the importance of different sociodemographic variables to male-female interactions, I used a linear model analysis of the frequency data. I chose a discrete regression model (Poisson regression) that computes parameter estimates using maximum likelihood methods (McCullough and Nelder 1983). The Poisson distribution is the basic distribution for count data and Poisson regression uses a Poisson-distributed error term. Frequency of a behavior for a male-female dyad was used as the dependent variable and sociodemographic characteristics of the male and female were used as independent variables. A separate analysis was performed for each behavior.

All sociodemographic variables I considered, except female reproductive value, were categorical variables with discrete rather than continuous distributions. Parameter estimates for categorical variables indicate the magnitude of an effect that can be assessed for statistical significance using T-tests. Reproductive value and frequencies of other social interactions were included as continuous variables and resulting parameters were tested against the null hypothesis that the parameter was equal to 0 using T-tests.

A stepwise regression procedure was used in each analysis. First an overall mean was fit to the data and then each independent variable was added separately to the model. A variable was considered for inclusion in a model if (1) it resulted in a significant ($P<0.05$) improvement in the percent of variance accounted for by the model, (2) resulted in the smallest mean square error of variables considered, and (3) accounted for at least 5% of the total variance in the data. The variables that accounted for the most variance were sequentially included in the model. Variables were included in the model until the addition of variables failed to satisfy criteria for inclusion. This method allowed me to evaluate the relative importance of the independent variables based on the percent of the total variance in the data attributed to each variable.

I compared the results of regression models for each behavior to determine if sociodemographic variables were consistently important across behaviors. I define a consistent effect as a variable that accounts for a significant amount of the variability for at least 2 behaviors. A consistent variable can be considered as being an important effect on general interactions with males whereas a significant but inconsistent variable is important for a specific type of interaction.

After the effects of independent variables in a model are accounted for, a significant amount of variability may

remain in the residuals (observed error). This may indicate that one or more variables have not been considered in the model (detected as nonrandom patterns in a residual plot) or that certain female-male dyads are interacting more or less than the model predicts (detected as outlier points on a residual plot). I identified male-female dyads with large, positive residuals, defined as more than 1 standard deviation (SD) above the mean standardized residual (Neter and Wasserman 1974), and rated them as moderate (between 1 and 2 SD) or strong (>2 SD). The residuals are used to identify dyads that interact more than expected based on the model. Classes of dyads that interact more than expected in more than 1 behavioral category are composed of individuals that have special relationships (Seyfarth 1978b; Altmann 1980; Smuts 1985). I generalize the definition of special relationships to include agonistic relationships as well as affiliative relationships.

Results

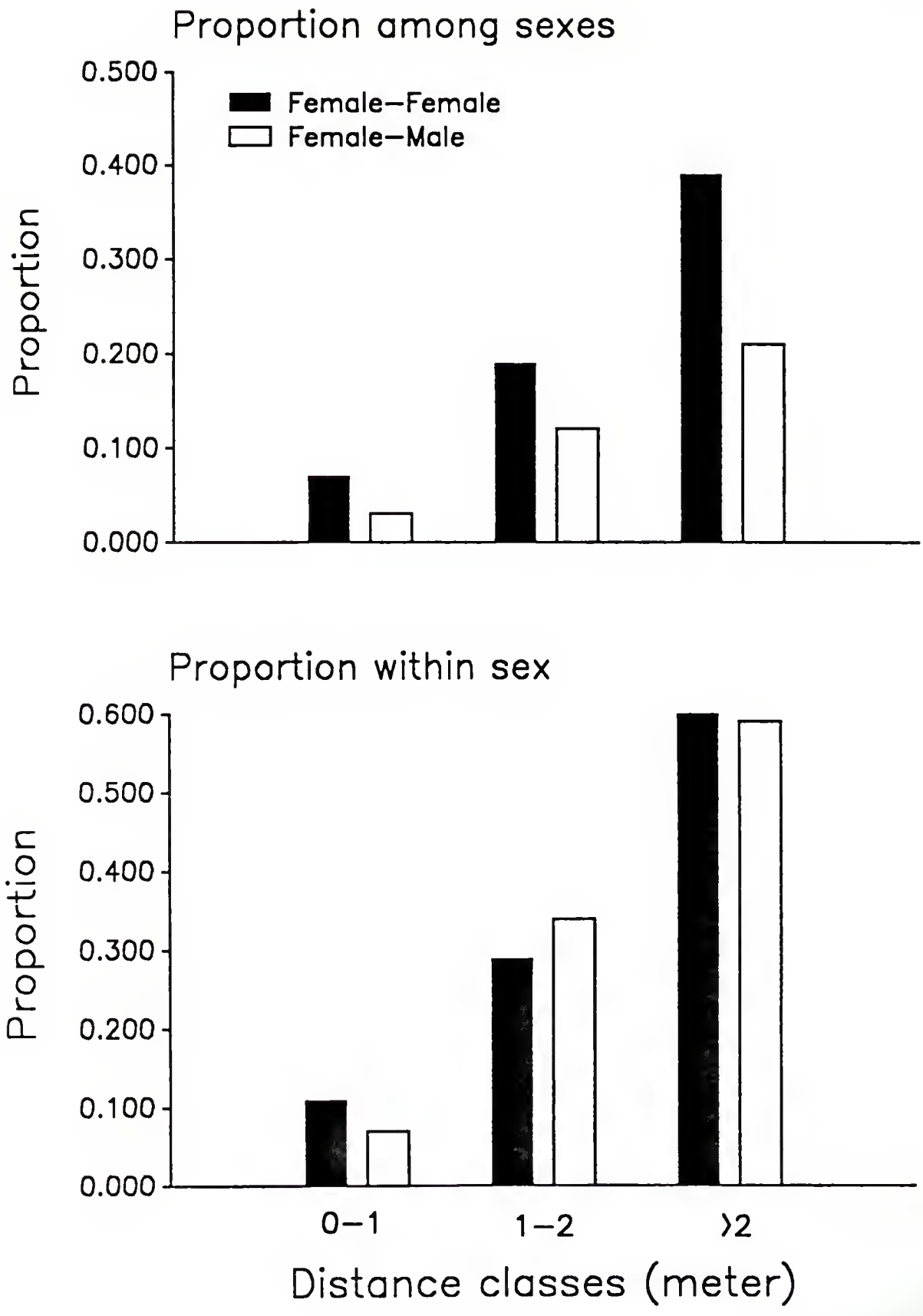
To evaluate whether the social relationships of females with males differ from relationships with other females, I first examined the spatial proximity of females to females versus males, and how females distribute affiliative and aggressive behavior between males and females. If a female capuchin monkey does not discriminate socially between males and females, then the frequencies and distributions of nearest neighbor distances should be similar for the two

sexes. The distributions of social interactions should also be similar if females are not discriminating between the sexes.

Distributions of Nearest-Neighbor Distances and Social Behaviors

When all groups were combined, females were nearest neighbors to females 64.4% of the time (1589 of 2469 observations) versus 52% expected under an hypothesis of random association. Females were 1.7 times more likely to be within 2 meters of another female than a male (Fig. 4.1). The distributions of nearest-neighbor distances for females and males were significantly different from the expected distributions for the pooled data ($G=9.03$, d.f.=2, $P<0.01$) and for each group tested independently ($P<0.001$). The sex-specific distribution of distances, however, is very similar. Females were within 2 meters of females for 40% of the female-female nearest-neighbor distances and were within 2 meters of males for 39% of the female-male nearest-neighbor distances. These results indicate that females spend more time in the proximity of females than of males, but that the distributions of nearest-neighbor distances for females and males are similar. If female do not discriminate socially between the sexes, then females might be expected to interact more often with females than with males as a result of the spatial proximity alone.

Figure 4.1. Distribution of nearest neighbor distances for female capuchin monkeys expressed as proportion of observations at 3 distance classes. Proportion among sexes is the distribution of all observations. Proportion between sexes is the distribution of female-female observations and female-male observations calculated separately.


Proportion among sexes
Female–Female
Female–Male
Proportion
0.500
0.400
0.300
0.200
0.100
0.000
Proportion within sex
Proportion
0.600
0.500
0.400
0.300
0.200
0.100
0.000
0–1
1–2
>2
Distance classes (meter)

To determine if females were discriminating between males and females in the group, I first tested the overall distribution of female-female and female-male interactions against a random distribution based on the number of potential interactants (dyads) of each sex available and against a distribution based on the relative rates that males and females were nearest neighbors (Table 4.1). Females are significantly more likely to interact with females than with males based on the number of potential interactants ($G=57.67$, d.f.=2, $P<0.001$) and based on spatial distribution of interactants ($G=58.99$, d.f.=2, $P<0.001$). The pattern of social interactions suggests that females discriminate between males and females. Females groomed with females 2.6 times as often as with males, were involved in aggressive encounters with females 1.3 times as often as with males (calculated by number of agonistic encounters between females divided by number of agonistic encounters with males or 222/170), and were supplanted by females as often as by males (Table 4.1). Females groom with females preferentially, but are involved in agonistic encounters and supplantations equally often with females and males.

Variation in Female-Male Interactions

Agonistic and affiliative behaviors between males and females were not uniformly distributed across female-male dyads: of 96 possible dyads, supplantations occurred in 59 dyads and other interactions occurred in only 36 dyads.

Table 4.1. Observed distribution of 4 social interactions (grooming, aggressive, defensive, and displacement interactions) between female-female and female-male dyads, and the expected distributions of behaviors under an assumption of random interactions weighted by potential number of interactants, and random interaction weighted by nearest neighbor distances. Number in parentheses indicates the number of dyads included in the observed distribution and the weighting factor used in the expected distributions.

Distribution	Dyads	Grooming Session	Female Defensive	Female Aggression	Female Displacement
Observed	Female (103)	380	222	222	186
	Male (96)	147	73	97	185
Random/Dyads[1]	Female (0.52)	273	153	165	193
	Male (0.48)	254	142	154	178
Random/NND[2]	Female (0.64)	339	190	205	237
	Male (0.36)	188	105	114	134

1. Heterogeneity Chi-square=57.67, d.f.=3, P<0.001.
2. Heterogeneity Chi-square=58.99, d.f.=3, P<0.001.

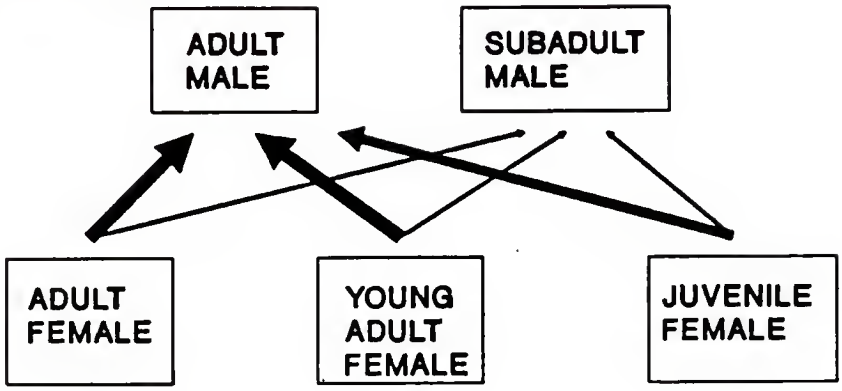
Females groomed males in 147 grooming sessions (Table 4.1), but adult males were the primary recipient of grooms. Subadult males were involved in more than 80% of male aggression toward females and 70% of female supplantations, but received few grooms (Fig. 4.2). The data indicate that females direct their affiliative behavior toward adult males and aggressive interactions occur primarily with subadult males. Because there were more subadult than adult males in the study, I next analyzed opportunities for interaction based on the relationship between nearest-neighbor distances and behavioral interactions for females and males.

I used an association index (AI) to measure the amount of association between a female and a male relative to that female's average association with other males in the group. I compared the number of times a male was the nearest-neighbor within 10 meters to a female to the average of nearest-neighbor distances for other males. The index increases from 0 when there is no association between a female and male upwards as the dyad spend more time as nearest neighbors. For White group, the index is undefined because only 1 male was present at any time during the study.

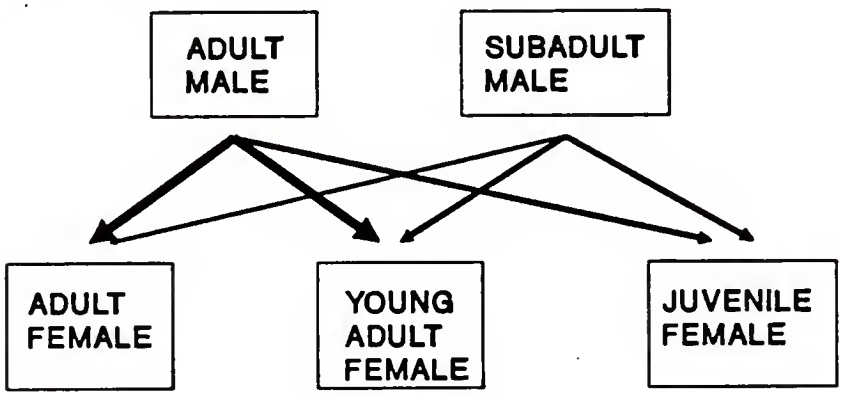
The average AI for Splinter and Main groups was 1.156 (SD=1.018, CV=88%; Fig. 4.3), showing that, on average, some males were much more attractive than others and there was considerable variability in AI. AI was weakly correlated

Figure 4.2. Distribution of social interactions between females and adult and subadult males by female age. All frequencies are expressed as number of interactions per dyad.

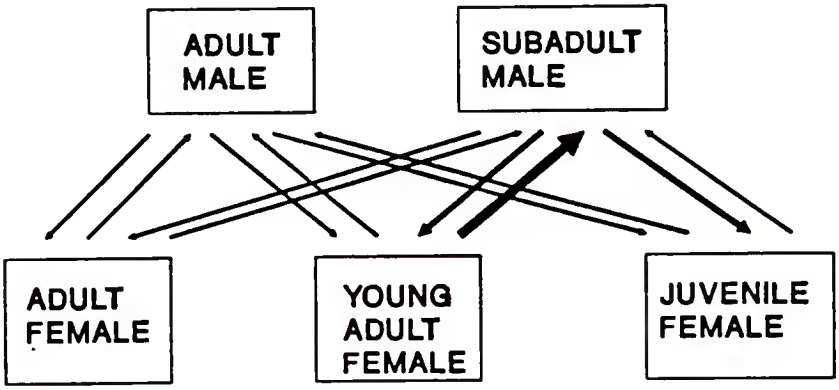
GROOMING SESSIONS



FEMALE DISPLACED

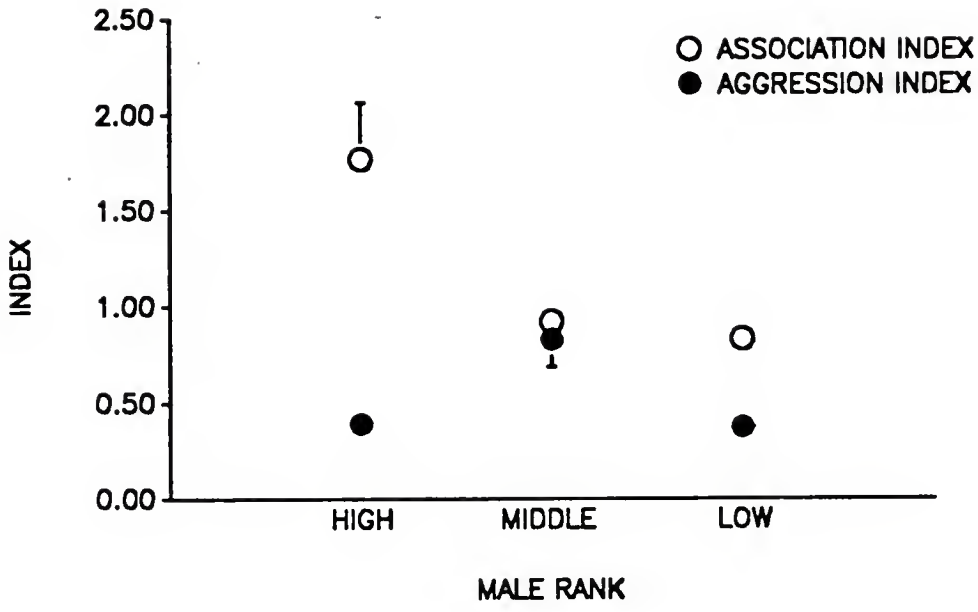


AGGRESSION



0-1 → 2-3 ➡
1-2 ➡ 3-4 ➡

Figure 4.3. Indices of association and aggression between females and high, middle and low ranking males.


2.50
2.00
1.50
1.00
0.50
0.00
INDEX
ASSOCIATION INDEX
AGGRESSION INDEX
HIGH
MIDDLE
LOW
MALE RANK

with increasing male rank ($r=0.34$, $n=92$, $P<0.001$) and number of grooming sessions ($r=0.39$, $n=92$, $P<0.001$), but not with other male/female characteristics or behaviors. Regression analysis of effects of sociodemographic variables on AI indicated a significant effect of male rank ($F=8.34$, $d.f.=2,87$, $P<0.001$). The AI of high-ranking, adult males (AI=1.77) was greater than that of medium-ranking (AI=0.92) and low-ranking (AI=0.83), subadult males. Females were twice as likely to associate with the dominant male in their groups as with the subordinate subadult males.

A second measure of association I used was an aggression index (AgI) described as a tolerance index by Robinson (1981). AgI is calculated as the number of aggressive interactions between a male and a female divided by the number of times they were nearest neighbors at less than 10 meters. This measure adjusts the frequency of aggression to variation in proximity of individuals. Low scores result when individuals are tolerant of one another whereas higher scores indicate either frequent fighting or low rates of association. AgI was not correlated with AI ($r=-0.18$, $P=0.09$) because there is a linear effect of declining male rank on AI, and a curvilinear effect of declining rank on AgI (Fig. 4.3). Regression analysis resulted in a significant effect of male rank ($F=5.77$, $d.f.=2,91$, $P=0.004$) and a marginal effect of female rank ($F=2.70$, $d.f.=2,91$, $P=0.071$) on AgI. High- (AgI=0.391) and

low- (AgI=0.392) ranking males were tolerated by females more than medium-ranking males (AgI=0.829). High- and medium-ranking females were more intolerant of males than low-ranking females (AgI equal to 0.615, 0.749, and 0.380, respectively).

The association index results suggest that females prefer to associate with the dominant male more than the lower-ranking subadult males. The aggression index suggests that females are most intolerant of middle-ranking subadult males, but tolerant of low-ranking subadult males. AI and AgI account for much of the difference in social interactions between males and females in large and small groups. Table 4.2 suggests that the primary difference in female-male interactions in large and small groups is that males in large groups are more aggressive toward females. If only interactions with the dominant male are considered, the difference in male aggression toward females is reduced significantly and the primary difference becomes rates of grooming between females and the dominant male in small and large groups. This suggests that the frequency of male aggression toward females may be attributed to the number of subadult males present whereas grooming interactions are primarily a function of the number of females present.

The ratios and the differences in distributions of social behaviors between females and males suggest that the patterns of female interaction with males depend on male and

Table 4.3. Results of Poisson Regression of influence of sociodemographic variables on male-female interactions in capuchin monkeys. Values are percent of total variability accounted for by each independent variable, total variability accounted for by the model, and the significance of residual variation. Dependent variables are frequencies of displacements, female aggression toward males, male aggression toward females and grooming sessions.

Independent Variable	DF	Displacement	Female Aggression	Male Aggression	Grooming Session
Female Rank	2	--	18.2%	--	24.0%
Male Rank	2	5.7%	15.6%	--	31.5%
Displacement	1	--	--	19.3%	--
Defensive	1	23.6%	--	--	--
Total		29.3%	33.8%	19.3%	55.5%
Residual		P<0.001	P<0.001	P<0.005	P<0.001

female characteristics, group size, and the behavior considered. I therefore examined the characteristics of males and females to determine which sociodemographic variables were important determinants of each type of social interaction.

Determinants of Social Interactions

I used a discrete linear regression model to assess the importance of sociodemographic characteristics of males and females on the 4 types of female-male interactions. I also examined how much variability in one behavior could be accounted for by treating other behaviors as covariates. Female reproductive value, female age, relatedness between males and females, male age, classification of males born in group versus immigrant, male age, and group membership were not significant factors for explaining variability in the social interactions considered. Frequency of female aggression and frequency of grooming were not significant as covariates for other female-male interactions.

Male and female rank accounted for most of the variability in female aggression toward males and grooming sessions (Table 4.3, Fig. 4.4), two behaviors that are initiated by females. High-ranking females were significantly more likely to be aggressive toward males than middle- or low- ranking females, and middle-ranking females were more aggressive than low-ranking females. High-ranking females also groomed males significantly more often than

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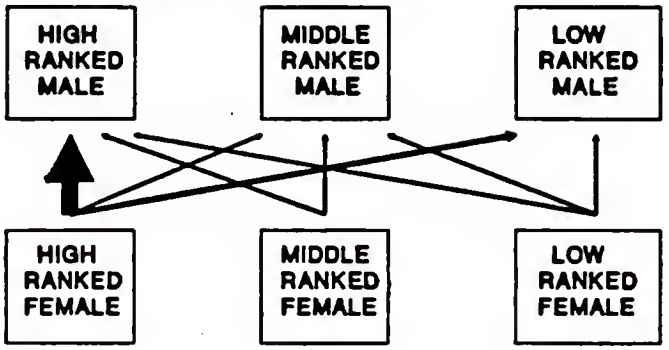
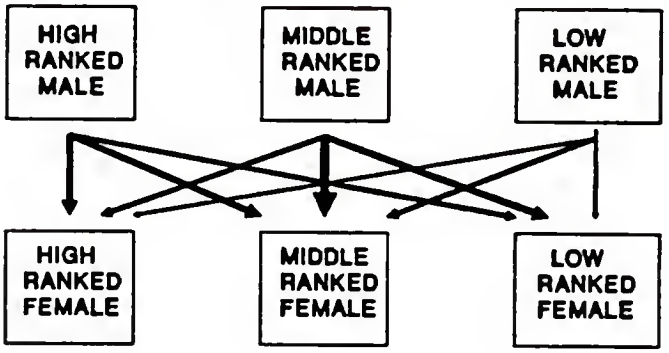
Male Rank	2	5.7%	15.6%	--	31.5%
Displacement	1	--	--	19.3%	--
Defensive	1	23.6%	--	--	--
Total		29.3%	33.8%	19.3%	55.5%
Residual		P<0.001	P<0.001	P<0.005	P<0.001

Figure 4.4. Distribution of social interactions between females and males by female and male rank. All frequencies are expressed as number of interactions per dyad.

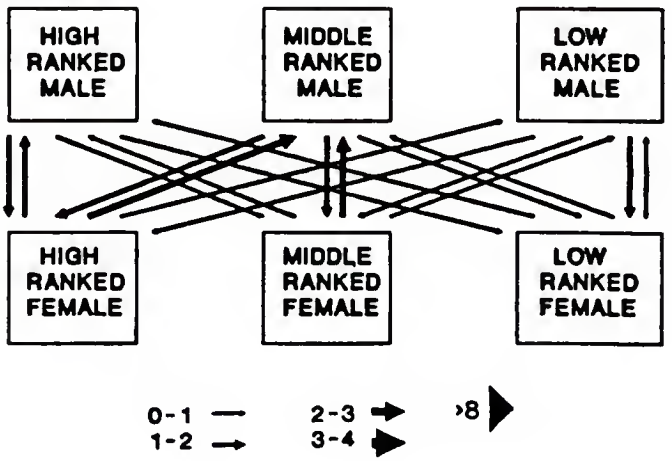
GROOMING SESSIONS



FEMALE DISPLACED



AGGRESSION



middle- or low-ranking females. The dominant male was least likely to be a victim of female aggression, and middle-ranking males were most often the target of female aggression. High- ranking, adult males were targets in only 5% of female aggressions whereas middle-ranking, subadult males were targets in 49% of interactions. The dominant males received grooms from females significantly more often than middle- and low-ranking males (74% of all grooming sessions) and low-ranking males received grooms significantly more often than middle-ranking males (22% versus 4%). High-ranking females groom the dominant male and are aggressive toward the lower-ranking males, especially the middle-ranking males. Middle-ranking females are aggressive toward middle- and low-ranking males. Low-ranking females do not often initiate interactions with males.

Female and male ranks are less important in accounting for variability in behaviors that are initiated by males (Table 4.3, Fig. 4.4). High-ranking and middle-ranking males are significantly more likely to supplant females than are low-ranking males, but male rank only accounts for 5.7% of the variability in supplantation. Male aggression toward females is a significant positive covariate of supplantation and accounts for 23.6% of variability in supplantation. Similarly, supplantation accounts for 19.3% of the variability in male aggression. Male-initiated behaviors toward females are correlated to the extent that males tend

to be aggressive toward females that they also are supplanting. Middle- and high-ranking males account for 52% and 32% of females supplantations, respectively. Middle-and low-ranking males account for 50% and 29% of male aggressions, respectively. The middle-ranking males have a consistent pattern of agonistic behavior whereas the high-ranking male supplants females more than low-ranking males and is aggressive toward females less than low-ranking males.

Significant amounts of residual variation remained after accounting for sociodemographic effects and behavioral covariates in the 4 regressions described above (Table 4.3). Large positive residuals indicate that certain male-female dyads are interacting more often than predicted by the model. An examination of large positive residuals, partitioned by female and male rank (significant sociodemographic variables in the regressions) indicates that the models do not fit well for certain rank classes (Table 4.4). Middle-ranked females are supplanted more often than expected whereas high- and low-ranking females are aggressive more often than expected. High-ranking females are also targets of male aggression more often than expected. Models appear to predict interactions between females and high-ranking males well, but interactions with medium-ranking males often exceed predicted values. Within behaviors, middle-ranking males account for 50 to 70% of

Table 4.4. Number of residuals greater than the mean standardized residual for female-male social interactions in capuchin monkeys. Residuals are classed by female and male rank for 4 behaviors.

Female Rank	Male Rank	Displacement		Female Aggression		Male Aggression		Grooming Session	
		1-2SD	>2SD	1-2SD	>2SD	1-2SD	>2SD	1-2SD	>2SD
High	High	1	--	1	--	1	--	1	1
	Medium	--	--	2	2	1	3	--	--
	Low	1	1	2	--	1	--	--	1
Medium	High	--	--	--	--	--	--	--	1
	Medium	3	1	--	2	2	--	2	--
	Low	2	--	--	--	--	1	--	1
Low	High	1	--	--	--	--	--	--	1
	Medium	1	1	3	1	1	--	3	1
	Low	--	--	--	1	1	1	--	1

residuals exceeding 1 SD, indicating that the models underestimate interactions with these males. Across behaviors, 85 to 87% of frequencies of interactions for male-female dyads fall within 1 SD of the values predicted by the regression models.

The regression models explain from 19% to 55% of the variability in female-male interactions. Behaviors that tend to be initiated by males were less predictable than behaviors that were initiated by females. Male age and rank tend to be confounded because rank is a function of size in capuchin monkeys. Age and rank effects in females are also confounded because of personality differences in the females and because females have a rank relationship to males (Robinson 1981). Certain females tend to avoid interactions with males by occupying a peripheral position in the group, whereas other females (especially young adults and juveniles) occupy central positions in the group and interact more often with males. Females also form coalitions against males that obscure the nature of agonistic interactions when dyads are the unit of measure. Some females have consistent agonistic relationships with certain males that exceed expectation based on the model and other females have strong affiliative relationships with the dominant males. These relationships are not predictable as a function of the parameters reported in this analysis. Such individual variability in behavior of males and females

reduces the predictive capabilities of models that are based on classes of individuals. Models that include male and female identities would be expected to account for more of this individual variability.

Discussion

The fundamental assumption of this paper is that the costs and benefits of group living are reflected in the social relationships of individuals in a group. Females are expected to be affiliative to those individuals that provide the greatest benefits and to avoid individuals that represent costs. The data presented here provide strong evidence that females differentiate socially between males. Females tend to avoid males and to concentrate their affiliative relationships among themselves. When interacting with males, females prefer the dominant adult male. Females avoid or are aggressive toward lower-ranking subadult males. Affiliative patterns suggest that most benefits of males accrue through the dominant male. Patterns of aggression and supplantation indicate that middle- and low- ranking subadult males are the more costly males.

Male Quality and Social Interactions

Female social interactions with males may be understood in terms of the relative qualities of males and the benefits that males offer to females. Males can offer a female genes that maximize fitness of offspring, access to resources and parental care of young (Robinson 1982; Janson 1984). While I

cannot differentiate the relative importance of these alternatives in terms of fitness effects for the female, I will discuss the plausibility of these factors given the current knowledge.

In C. olivaceus, males occasionally provide infant care (Robinson and Janson 1986; O'Brien unpubl. data) but there is no clear pattern of aid giving by adult, subadult and juvenile males. Alloparental care by males may be associated with number of nulliparous females present; Robinson (pers. comm.) observed extensive male care when few nulliparous females were present in a group, whereas I observed only occasional male care in the same group when many nulliparous females were present. Alloparental care by the adult male has only occasionally been observed in C. olivaceus, mainly in small groups. Male alloparental care is more common in callithricids where kinship effects (and possibly polyandry) are important (Vogt et al 1978; Hoage 1982; Goldizen 1986), and in Papio sp. where males become involved in complex relationships with mothers and infants (Altmann 1980; Whitten 1986). The lack of consistent patterns of alloparental care by subadult and adult males suggests that such care is not a reliable quality by which females might judge males.

Males improve females access to resources as a group. Robinson (1988a, b) and Srikosamatara (1986) showed that the outcome of group encounters is a function of increasing

group size and the number of adult and subadult males in the group. The distance moved increased and time spent resting decreased after losing an encounter and represented an energetic cost of losing group encounters. Robinson also demonstrated that females in large groups have higher fecundity and reproductive success than females in small groups. Females appear to gain a fitness advantage as a result of male presence in the group but it is unclear whether the advantage results from size of males in groups, number of males, or some combination.

Within groups however, males compete with females for food resources. While this competition is mitigated somewhat by partitioning of the vertical foraging space (Robinson 1986), many supplantations and aggressive interactions occur during foraging. Agonistic encounters with males occur 1.6 times more often during female foraging than other times, whereas agonistic encounters among females are equally likely to occur during foraging as at other times. Of 86 aggressive interactions and 131 supplantations recorded during focal samples in which context of the interaction could be determined, 45 aggressive and 91 supplantation interactions interrupted female foraging bouts. During focal samples in which foraging exceeded 50% of the total sample, females foraged 6.6% longer in the absence of supplantations or aggressive interactions involving males. The dominant adult male was as agonistic toward females as was the

average subadult male during foraging bouts. Feeding in the proximity of the dominant male is as risky as feeding near subordinate males and it is therefore unlikely that a female would choose an adult male based on improved access to resources.

The dominant adult male performs all of the effective breeding in C. olivaceus (Robinson 1988b) and this may be the primary reason to associate preferentially with the dominant male. Females usually initiate interactions with the dominant male, approaching to groom him although he rarely reciprocates, competing for opportunities to groom him and soliciting him for copulation (Robinson 1981, see below). Grooming solicitations of other males are usually ignored. I observed one subordinate male assume the dominant position in Main group, resulting in a dramatic change in his social relationship with females. Females started grooming him, aggressive interactions declined considerably, but rates of supplantation remained relatively constant. The male's new dominance status was accompanied by a new affiliative relationship with group females. This male then sired offspring the following spring. It seems therefore that a benefit provided by the dominant male that subordinate males do not offer is insemination.

There are 3 reasons why insemination by the dominant male might be desirable: superior genetic quality of the dominant male, protection of offspring by dominant male, or

high cost of mating with subordinate males. There is no evidence that female primates choose males based on genetic superiority (Smuts 1986). Most field studies of vertebrate organisms are not designed to address genetic aspects of individual differences and therefore rely on phenotypic expression of traits to infer genetic quality. Dominance status may not be a good predictor of genetic quality in cebids because genetic differences between males may be small (Janson 1984) and because many environmental and social factors influence dominance status. Whether the dominant capuchin male is a genetically superior male cannot be answered for C. olivaceus at this time.

A second, but perhaps more important factor influencing choice of the dominant male as mate is that the dominant males are known to be intolerant of infants that they have not sired. New dominant males have been observed to commit infanticide upon taking over a group (Valderrama et al. in press), but subordinate males are not known to be aggressive toward infants. Presumably, a male can differentiate between infants he has sired and those he has not. If mating with a subordinate male increases the chances that the resulting infant will be injured or killed by the dominant male, then a female improves the probability of survival of her infant if she restricts mating to the dominant male only. Preference for the dominant male may represent a compromise

between mating with a "best" male and the risk of wasting a reproductive attempt if the infant is killed.

Female Rank Affects Social Interactions with Males

Social interactions that are initiated by the female are affected by female rank. High-ranking females (especially young-adult and adult females) monopolize the grooming sessions with the dominant male at the expense of other females. Other males are ignored. In Main group (but not in small groups), high-ranking females disrupt grooming sessions and chase females that attempt to move close to the dominant male (see O'Brien Chapter 3). The extreme asymmetry in grooming of the dominant male suggests that high-ranking females effectively control access to the dominant male when many females are present and may be an expression of female-female reproductive competition (Seyfarth 1978b). By restricting access to the dominant male, high-ranking females attempt to monopolize the primary benefits of having males in the group. Middle- and low-ranking females are essentially denied the opportunity to develop a social relationship with the dominant male but are subject to all the costs of female-male aggression. The benefits of having males in a group, as reflected by affiliative social relationships, are concentrated among the dominant females of the group.

High-ranking females are more aggressive toward males. They are more likely than lower-ranked females to attack a

male that has either approached, supplanted, or antagonized them. Although supplantations and aggressions tend to occur independent of female rank, high-ranking females suffer relatively fewer incidents than middle- and low-ranking females. Aggression toward males may represent an attempt to reduce male aggression by increasing the risk of reciprocity.

Comparisons with Brown Capuchin Monkeys

Janson (1985) emphasized the importance of within group competition for food as a driving factor in the social organization of brown capuchin monkeys (Cebus apella) in the Manu National Park in Peru. Dominance rank was the most important factor affecting food intake at resources where levels of fighting were high. At food sources where little fighting occurred, level of aggression received affected food intake more than dominance rank. Animals could increase food intake by avoiding competitors as well as by being high ranked. Aggression and supplantation during foraging appears to affect a female's time spent foraging in C. olivaceus (see above). Male aggression toward females may be mitigated somewhat by high female rank or by avoiding males by foraging at the periphery of the group (see O'Brien Chapter 3). Agonistic encounters between males and females often occur in a nonforaging context, however, and should be viewed as a social cost as well a cost of food competition.

Janson (1984) also proposed that the dominant male's control of food resources allows it to offer benefits to females and offspring that subordinate males cannot. Female preference for the dominant male may explain why brown capuchin groups are multimale since additional subordinate males may increase the dominant male's access to females while causing minimal mating competition. In C. olivaceus, groups are primarily single male with nonbreeding subordinates males. The dominant male's intolerance of infants sired by other males may make it pointless for females to mate with subordinate males. There is little evidence to suggest that females improve access to resources by foraging near the dominant male. More work is needed on the mating system of C. olivaceus to clarify the costs and benefits involved in mate choice.

Do females compromise the benefits of group living by tolerating males in the group? The dominant male is certainly important as the primary or only breeder and for assistance in group defense. Low-ranking females, however, do not develop affiliative social relationships with the dominant male. Subadult males contribute to group defense, but are aggressive toward and supplant females. Competition for food is probably an increasing problem as number of males in a group increases. The extent to which females can form coalitions against aggressive males, and control male immigration and emigration may provide more information on

the costs and benefits of males to group-living females. This study suggests that while dominant males are important to female capuchin monkeys, the role of the nonbreeding male is more ambiguous, involving tradeoffs between benefits accrued through access to resources and costs of competition and aggression.

CHAPTER 5

INFANT CARE AMONG FEMALE WEDGE-CAPPED CAPUCHIN MONKEYS: EFFECTS OF AGE, RANK, AND RELATEDNESS.

Introduction

Primate infants are born in an altricial state, and the degree of infant care is a major correlate of infant survival. In many primates, allomaternal care is an important element of infant care (see Reidman 1982; Nicholson 1986 for reviews of alloparental care), but the level of allomaternal care varies considerably among species. Nilgiri langurs (Presbytis nilgiri), for example, have a very short maternal investment, supplemented by erratic allomaternal care (Poirier 1968). Hanuman langurs (Presbytis entellus: Hrdy 1977, 1978) participate in extensive allomaternal interactions, but not all of it is beneficial. In yellow baboons (Papio cynocephalus), mothers tend to restrict access to infants during the first 3 months, when monthly infant mortality is the highest (Altmann 1980) and allomaternal care (excluding investigation of infants) is relatively low. Some callithricids, however, exhibit well developed maternal and

allomaternal care patterns (Terborgh and Goldizen 1985; Goldizen 1986).

Several factors influence whether care is provided by mothers or allomothers. Maternal care may be limited by the energetic requirements of the mother (Altmann 1980; Terborgh and Goldizen 1985). Allomaternal care reduces the energetic demand imposed on the mother by the infant. McKenna (1979, 1982) postulates that diet and the development of female dominance hierarchies determine the nature of allomaternal care in primates. The availability of allomothers of the right age, rank, and relatedness in a group is fundamental to the development of allomaternal care and is a function of demographic processes. Age-specific survival, sex-specific survival, dispersal, and genealogical patterns determine whether females are present in a group and available as potential allomothers.

What determines these demographic characteristics? One factor is the degree of infant care. As infant care increases, infant survival increases, and more individuals enter the juvenile and adult age classes (and become available allomothers). This positive feedback results in a high probability that an infant has older siblings and more distant relatives in a group, and these relatives are likely candidates for giving allomaternal care. One might expect, therefore, that species having high infant survival and female philopatry will also have strong allomaternal care.

The wedge-capped capuchin monkey (Cebus olivaceus) is such a species.

The wedge-capped capuchin monkey is an excellent species for studying patterns and mechanisms of infant care. Infant survival is high, females rarely disperse, matrilines vary in size, and groups vary in average degree of relatedness (Robinson 1988a, 1988b). Capuchins are characterized by an unusually high level of allomaternal care that persists longer than is typical of Old World species and includes related as well as unrelated females. Is high infant survival related to allomaternal care in capuchin monkeys? A demonstration that allomaternal care accounts for a significant portion of infant care or is given at crucial times (e.g. when maternal care is declining) would suggest that allomaternal care is important. Altmann (1980) found that second year mortality in yellow baboons was comparable to first year mortality. She suggested that extension of infant care in the second year might increase the rate of survival of infants. If infant survival increases as the result of receiving allomaternal care, what mechanisms might account for such behavior?

Theories concerning the evolution of allomaternal care are based on benefits and costs for the participants, evaluated in units of fitness gained or lost. Under kin selection mechanisms (Hamilton 1964; Brown 1987), related

allomothers and the infant should benefit from allocare and relatedness should be the primary determinant of allomaternal care. If allocare is altruistic (Hamilton 1964; Trivers 1971; Bertram 1982), the behavior should be costly to the allomother (or benefits would be delayed) but beneficial to the infant. Relatedness should not be important. One might expect juvenile and young adults to participate more than adults because younger age classes are more likely to benefit in the future from additional animals in the group. One would also expect low-ranking females to participate more than high-ranking females since low-ranking females may benefit more from helping a high-ranking infant than vice versa. If allocare is purely selfish behavior, as proposed by Hrdy (1977), it should benefit the allomother at the cost of the infant. Relatedness should not be important. Younger animals should participate more since they presumably benefit from the experience, and the allomothers should be high-ranking females caring for low ranking infants. Low-ranking females should not have access to high-ranking infants if behaviors are costly to infants. These 3 ideas can be distinguished in a 2-step process: an effect of relatedness discriminates between kin selection and altruistic or selfish behavior; the direction of an effect of rank distinguishes between selfish and altruistic behaviors.

This paper examines patterns of infant care in capuchin monkeys and attempts to distinguish the mechanisms promoting allomaternal care. I describe the behaviors associated with maternal and allomaternal care, consider the time course of these behaviors as reflected by the age of the infant, and evaluate the relative importance of female age, rank, and relatedness as they affect a female's interactions with infants.

Methods

I studied the females in 2 small groups and 1 large group of wedge-capped capuchin monkeys. Dominance hierarchies and genealogies were known for all groups and all individuals were recognizable. White group contained 3 adult females (mother and 2 daughters), and two 18-month old males at the beginning of the study. Two additional male infants were born during the study. Splinter group contained 2 adult females (probably first cousins), an unrelated adult female, and an old juvenile daughter of the dominant female. There were one 18-month old and two 6-month old males at the start of the study, and a male and a female infant were born during the study. Main group was composed of 6 adult, 3 young adult, 3 old juvenile, and 2 young juvenile females. The young juvenile females spent the first 6-months of the study classed as old infants. The females were organized into 5 matrilines and degrees of relatedness between matrilines were known. There was one 18-month old male and

two 18-month old females at the start of the study. Three male infants were born into the group during the study. Three females were pregnant but lost infants shortly after birth. These infants were never directly observed or sexed. Of the infants included in the study, 2 males from Splinter and 2 males from Main groups disappeared and presumably died.

Additional data collected by Robinson (unpubl. data) in 1977 and 1978 for Main group were analyzed. These data contain information on frequency of nursing and carrying for 9 adult females, 3 juvenile females, 4 male infants, and 4 female infants. Eight Main-group females present in 1986-88 as adults also were present in the earlier data.

I collected data for 15 months (December 1986 to March 1988). Behavioral observations began as soon as females were recognizable, usually between 0600 and 0630, and lasted for 12 hours. Observations consisted of a 20-minute focal sample on an individual female, followed by a 20-minute scan sample of the group and a 20-minute opportunistic sample each hour (Altmann 1974). Females were sampled systematically such that each female was included in a focal sample in each of three 4-hour time periods (morning, midday and late afternoon). During the first 12 months of sampling, I recorded all behaviors that lasted at least 3 seconds during a focal sample. For the last 3 months I recorded only social/agonistic interactions. During opportunistic samples,

I recorded all observed social/agonistic interactions involving females. During scan samples, I recorded the activity of as many individuals in the group as I could observe in 20 minutes. I also recorded nearest neighbor, height from the ground, food item if foraging, and proximity of infants. I was usually able to observe all individuals in a small group and approximately 80% of the individuals in the large group in a given scan sample. I combined the data from the 3 sampling regimes for analysis of frequency of behaviors.

I analyzed 4 types of maternal and allomaternal behaviors:

1. Investigation. This behavior occurred during first 2 months of the infant's life while it was being carried by the mother. Females would sniff, mouth, and touch the infant and gently pull on the tail. Often the anogenital area was muzzled. Mothers never investigated their own infant.
2. Nursing. Infant would take the nipple of a lactating female to its mouth. I was not able to determine if infant actually sucked nipple in every case. Mothers and allomothers nursed infants.
3. Carrying. Infant would cling dorsally to a female as the female moved or engaged in other activity. Mothers and allomothers carried infants.
4. Association. All activity (excluding above) during which a females's attention was directed toward an infant or

involved a close spatial proximity to one or more infants. These activities included babysitting (Robinson and Janson 1987), resting, grooming, and playing with infants, and infant following a female during group progressions.

For each behavior I recorded the identities of interactants and the frequency that the behavior occurred between a dyad. I analyzed the frequency of interaction for each behavior for the effects of infant sex, infant age, infant rank relative to the female, female age, female rank in the group, degree of relatedness between interactants, and group identity. These are called sociodemographic variables. Because rank and kinship are correlated (ranks of related females are clustered), I use the measures of female rank in the group and infant rank, which is the rank of the infant in relation to the interacting female's matriline.

First, frequencies of all 4 behaviors in the 1986-88 data set were combined to test (using G-tests) for overall effects of kinship, female age, and female rank relative to the infant. Females were classified using kinship, with categories of close kin ($r=0.5$), distant kin ($0.5>r>0$), and nonkin ($r=0$); using age, with categories of young juvenile, old juvenile, young adult (nulliparous), and adult; and using rank, with categories of rank below the infant, rank above the infant, or rank equal to the infant. Females classified as having equal rank were invariably siblings because an infant's rank within a matriline is often

undetermined. Since kinship, age, and rank are tested independently, the results measure only if an effect is significant and do not measure the relative contribution of the different effects.

To assess the relative importance of different sociodemographic variables, I used a linear model analysis of the frequency data. I used a discrete regression model (Poisson regression) that computes parameter estimates using maximum likelihood methods (McCullough and Nelder 1983) using an error term with a Poisson distribution. This method is analogous to least-squares regression for continuous, normally distributed data. Frequency of behavior for a female-infant dyad was used as the dependent variable and sociodemographic characteristics of the infant and female were used as independent variables. A separate analysis was performed for each of the 4 behaviors in the 1988 data set and for the 2 behaviors in the 1978 data set, for data sets that included the mother-infant interactions and for data sets that included only allomaternal interactions.

Continuous (ages, rank) and categorical (relatedness, sex) variables were entered in the models. Categorical variables result in a set of parameters whose actual values are meaningless for prediction but whose relative values indicate the importance of an effect. For example, a high (parameter) value for category of close relatedness (r=0.5) versus other classes of relatedness indicates an effect of

kinship. Because infants were born or died or entered the juvenile age class at different times, they were available for interaction with females for different amounts of time. I used the number of months that an infant was present in the samples as a weighting factor in the analyses to control for unbalanced samples.

A stepwise regression procedure was used in each analysis. First an overall mean was fit to the data and then each independent variable was added separately to the model. A variable was judged as 'best' if it resulted in a significant ($P<0.05$) improvement in the percent of variance accounted for by the model, resulted in the smallest mean square error, and accounted for at least 5% of the total variance in the data. Models were developed by adding variables, one at a time, until no further improvement in the model was obtained. This method allowed me to evaluate the relative importance of the independent variables as a function of the percent of the total variance in the data attributed to each variable. Evaluation of the parameter estimates depended on whether the independent variable was continuous or categorical. Continuous variables were evaluated by their sign and the relative importance in the model. Categorical variables were interpreted by the magnitude of the differences in the parameter estimates and by relative importance in the model.

I compared the results of regression models for each behavior in each data set to determine if sociodemographic variables were consistently important across behaviors, across data sets that included and excluded mother-infant dyads, and across the 1986-88 and 1977-78 data sets. I define a consistent effect as a variable that is significant for at least 2 behaviors within a data set or significant across 2 data sets. A consistent variable can be considered as being an important effect on general interactions with infants whereas a significant but inconsistent variable is important for a specific type of interaction. Consistent sociodemographic variables may be considered as more important influences on female-infant interactions because the effect is generalized across behaviors and/or data sets rather than restricted to a single behavior.

After the effects of independent variables in a model are accounted for, a significant amount of variability may remain in the residuals (observed error). This may indicates that 1 or more variables have not been considered in the model (detected as nonrandom patterns in a residual plot) or that certain female-infant dyads are interacting more or less than the model predicts (detected as outlier points on a residual plot). I identified female-infant dyads with large, positive residuals, defined as >1 standard deviation (SD) above the mean standardized residual (Neter and Wasserman 1974), and rated them as moderate (between 1 and 2

SD) or strong (>2 SD). These residuals identified dyads that interacted more than expected based on the model and were described as social preferences (after Walters 1986). Dyads with social preferences in more than 1 behavior were termed special relationships (Seyfarth 1978, Altmann 1980, Smuts 1985).

Results

I observed 1286 interactions in the 4 behavior categories between females and infants in 1986-1988 (Table 5.1). Of these, 786 interactions (61.1%) involved mother-infant dyads. Mothers interacted preferentially with their own infants (x=87.1%, SE=0.070, n=9). Mothers would occasionally investigate or associate with another female's infant, but these interactions accounted for only 12.9% of a mother's total interactions. Sibling-infant dyads accounted for 205 (15.9%) interactions and other female-infant dyads accounted for the rest (23%). The ratio of interactions for mothers:siblings:other was 14.2:3.7:1.0. The results are similar when only allomaternal behaviors are considered; siblings account for 41.0% of the interactions and other females account for the rest.

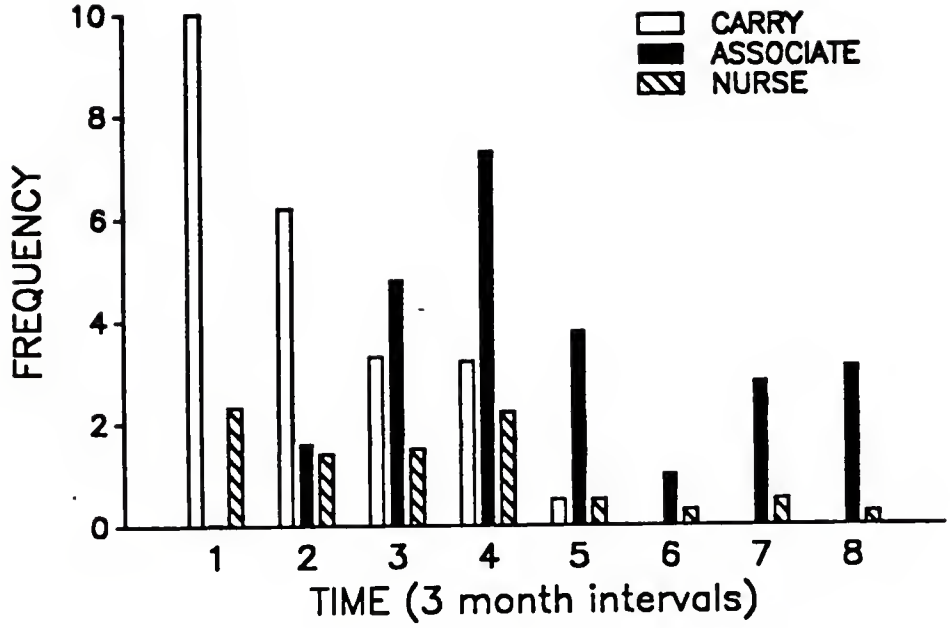
Maternal and allomaternal behaviors are affected by infant development. This is reflected in the changing frequency and nature of infant care as the infant ages (Fig. 5.1). Infants are carried and cared for almost exclusively by the mother in the first 3 months of life; 58.4% (258 of

Table 5.1. Frequency of maternal and allomaternal care by behavior, female age, and female relationship with infant (mother, sibling, rank) for 2 young juvenile, 4 old juvenile, 4 young adult and 11 adult females. Infant relationship with female is indicated as infant of female (INF), sibling (SIB), and rank of female relative to infants mother (I>F, I<F). Numbers in parentheses are number of potential female-infant dyads in each class.

Female Age[1]	Infant	Nurse	Carry	Assoc.	Inves.	Interactions per dyad
MO	INF (15)	101	443	252	0	52.4
YJ	SIB (2)	0	12	4	13	14.5
	I>F (1)	0	0	1	0	1.0
	F>I (3)	0	4	2	1	2.3
OJ	SIB (3)	0	19	30	5	18.0
	I>F (9)	0	10	10	1	2.3
	F>I (11)	1	24	63	35	11.2
YA	SIB (8)	3	37	47	33	15.0
	I>F (5)	0	0	1	0	0.2
	F>I (9)	3	5	12	11	3.4
AD	SIB (2)	0	0	2	0	1.0
	I>F (24)	5	10	19	9	1.8
	F>I (18)	1	6	26	35	3.8

1. MO=Mother, YJ=Young Juvenile, OJ=Old Juvenile, YA=Young Adult, AD=Adult.

Figure 5.1. Mean frequency per dyad of a) 3 maternal behaviors and b) 3 allomaternal behaviors in 3 month time intervals.


CARRY
ASSOCIATE
NURSE
FREQUENCY
0
2
4
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8
10
1
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3
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5
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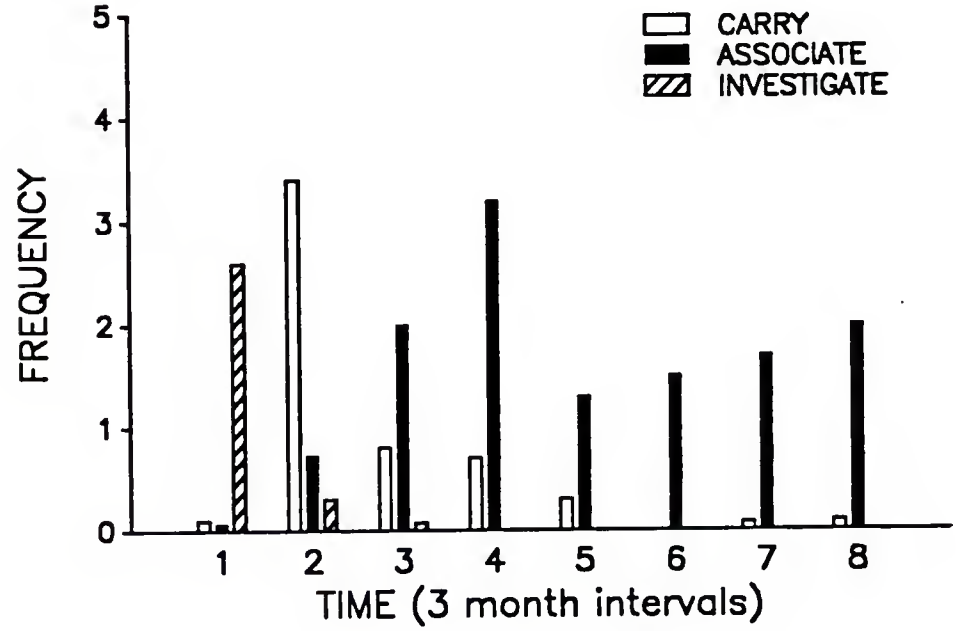
7
8
TIME (3 month intervals)


CARRY
ASSOCIATE
INVESTIGATE
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7
8
TIME (3 month intervals)

442) of maternal carrying occurred during this time. In contrast, I observed allomaternal carrying on only 2 occasions in the first 3 months. Investigation of infants by other females is restricted primarily to this time period. During months 4-6, the infant begins to move independently of the mother, but is still closely associated with her and allomaternal behavior, especially carrying, becomes an important part of infant care. For example, 79.3% (172 of 217) of the allomaternal carrying observations occurred during this time while maternal carrying declined to 22.9%. During months 7-9, the infant is associating with its mother and other females more than it is being carried by them. After the first year, maternal and allomaternal care decline and infants are relatively independent. Maternal nursing is rare after the first year of life and by 18 months of age infants were either weaned from their mother, or in the process of being weaned. Allomaternal nursing is rare at all times and does not follow the temporal pattern described above.

I first tested allomaternal behaviors for effects of rank, relatedness, and age by combining the 4 behaviors. The observed distribution of interactions among kinship categories was significantly different from expectation based on a random distribution of interactions ($G=248.24$, $d.f.=2$, $P<0.001$). Siblings and distant kin interacted more with infants than nonkin. The observed distribution of

interactions among age categories also was significantly different from expected ($G=127.14$, d.f.=3, $P<0.001$). Adult females interacted less than expected whereas old juvenile and young adult females interacted more than expected. Among rank categories, siblings interacted more with infants than high-ranking females and low-ranking females interacted least ($G=268.66$, d.f.=2, $P<0.001$). If siblings are eliminated from the analysis, the pattern remains the same: high-ranking females interacted more than the low-ranking females ($G=87.18$, d.f.=1, $P<0.001$).

Poisson Regression Analysis

The initial analysis shows that there are strong effects of relatedness, rank, and age on female-infant interactions. The analysis does not, however, permit the discrimination between the relative importance of these different factors on allomaternal behaviors. I therefore conducted a second set of analyses to address the question of relative importance.

For the 1988 data set with mother-infant dyads included (Table 5.2a), the effect of being a mother is apparent. Infants tend to nurse from females that they associate most with. Mother-infant interactions account for 88.6% of nursing and 53.7% of associations observed (Table 5.1). Association accounts for 63.7% of the variability in the nursing data and nursing accounts for 60.0% of the variability in the association data. Actual relatedness

Table 5.2. Summary of Poisson regression analysis of the influence of sociodemographic variables on 4 maternal/allomaternal behaviors for the 1987 data. A. dataset includes mother-infant interactions, B. data excludes mother-infant interactions. Values are the % variance accounted for by each variable, total variance accounted for by the model, and significance of residuals.

A.

INDEPENDENT VARIABLE	DF	NURSE	CARRY	ASSOCIATE
Female rank relative to infant	3	--	65.2%	10.4%
Relatedness	2	15.6%	--	--
Infant age	2	--	23.9%	8.8%
Nurse	1	--	--	60.0%
Associate	1	63.7%	--	--
Total variance		79.3%	89.1%	79.2%
Residual		sig.	sig.	sig.

B.

INDEPENDENT VARIABLE	DF	NURSE	CARRY	ASSOCIATE	INVESTIGATE
Female rank relative to to infant	2	--	--	24.5%	22.6%
Female rank in group	1	--	--	--	9.5%
Female age	3	--	5.8%	10.0%	--
Relatedness	1	--	30.0%	--	15.9%
Infant age	2	--	23.7%	15.4%	--
Group	2	--	--	--	10.5%
Associate	1	--	12.5%	--	--
Carry	1	6.1%	--	--	--
Total variance		6.1%	72.0%	49.9%	58.5%
Residual		sig.	sig.	sig.	sig.

accounts for 15.6% of the variability in the nursing data. Female rank relative to the infant also is important (accounting for 10.4% of variability in the association data), indicating that infants associate most with mothers, followed by siblings, high ranking females and low ranking females. The infant's age also has a slight effect on the frequency of association. Infants 6 months old at the start of the study were most likely to be involved in an association dyad. Younger infants are more likely to be carried by females than to be moving independently but in association with females (Fig. 5.1).

The frequency of carrying infants is most strongly influenced by the rank relative to the infant's matriline (65.2% of variability; Table 5.1a). Mothers are most likely to carry, followed by siblings. Unrelated females are least likely to carry an infant with the low-ranking females slightly more likely to carry than the high-ranking females. Given that the most closely related females are carrying the infant, the next most important influence on carrying infants is the infant's age. Old infants are least likely to be carried and young infants are the most likely to be carried.

In conclusion, when mother-infant dyads are included, infant care is most strongly influenced by kinship, especially through the mother-infant relationship. Where female rank relative to the infant is important, it is the

mother and sibling rank relationships that dominate the effect. There appears to be no effect of female age for any of the behaviors, although this is partly due to the strong effect of maternal behavior and all mothers are adults. The analysis shows strong consistency in that there is a maternal and/or sibling effect in all 3 behaviors and that infant age is an important effect in 2 behaviors that tend to be sequential over time. Although kinship appears to be more important than female rank, the analysis shows a difference in the nature of interactions involving high- and low-ranking females. High-ranking females tend to associate with infants and low-ranking females tend to carry infants.

To explore the effects of kinship, rank, and age on allomaternal care of infants, I eliminated the mother-infant dyads from the analysis (Table 5.2b) of the 1986-88 data. The frequency of allonursing was not influenced by any sociodemographic variables, but was weakly influenced by a positive effect of carrying. Allonursing was relatively rare (observed in 13 of 114 nursing interactions) and occurred in a variety of circumstances. Infants nursed from siblings and non-siblings, up rank and down rank, from pregnant females, from other mothers and from females that had recently lost their infants. Allonursing also involved old infants, who continued to nurse after entering the juvenile age class (juvenile nursing is called parasitic nursing; O'Brien, in press).

Allomaternal carrying was influenced most strongly by degree of relatedness (30.0% of variability; Table 5.2b), with siblings carrying infants most and unrelated females carrying least. The effect of infant age was the same as when mothers were included in the analysis (23.7% of variability); infants less than 6 months old are carried more than older infants. Females also tend to associate with the infants that they carry, but the associations occur later than the carrying (Fig. 5.1b), suggesting a change in the nature of female-infant relationships. Finally, there is a weak effect of female age for carrying. Old juveniles are most likely to carry infants, followed by young juveniles, young adults, and adults. Old juveniles are more likely to carry unrelated infants, whereas young juveniles and young adults carry siblings almost exclusively.

Female rank relative to the infant accounted for 24.5% (Table 5.2b) of the variability in the association data. Sibling females were most likely to associate with infants, followed by high-ranking females and then low-ranking females. The effect of infant age was the same as for the maternal/allomaternal data set with infants in the second 6-months of life most likely in association with females. Old juvenile females associate most and are most likely to associate with unrelated infants. Young-adult females are second most likely to associate with infants and direct most

of their attention to siblings. Adults and young juveniles are least likely to associate with infants.

The investigation of newborn infants was performed primarily by females of higher rank than the infant. Siblings investigated at an intermediate level and low-ranking females were least likely to be investigate infants. Females that were related to infants were more likely to investigate than unrelated females and females that ranked high in the group were more likely to investigate than low-ranking females. Finally, there was an effect of group. Females in the large group were much more active in investigating infants than the females in the 2 small groups.

The allomaternal care data show a strong effect of relatedness. Sibling females are consistently the most important category of allomothers that carry, associate, and, to a lesser extent, investigate infants. The effects of female and infant age are consistent for carrying and association. As infants age, they are carried less and in association more. The juvenile females tend to carry infants but the old juvenile and young adult females tend to associate with infants. Female rank relative to infants is consistent between association and investigation behaviors; high rank or being a sibling is necessary to gain access to infants. The first analyses, therefore, indicate that relatedness is the best predictor of interactions with

infants, followed by the female's rank relative to the infant. Although female age is important for some behaviors (Table 5.2), female age is not a strong predictor of female-infant interactions when compared to the female's relatedness and rank. These analyses also show that females interact with infants differently depending on the age of the infant and the behavior.

Repeating the analysis for the 1977-78 data on nursing and carrying including mother-infant dyads (Table 5.3a) and excluding mother-infant dyads (Table 5.3b) yields similar results to the first analysis. Degree of relatedness again was the principal influence when mothers were included for nursing and carrying. Infant sex affected the likelihood of nursing in the 1977-78 data, but was not important for any behavior in 1986-88. This results from the more balanced ratio of male to female infants in the earlier data (4:4 versus 12:3). Female infants were nursed more than males in 1977-78 and mothers nursed their own infants more than unrelated infants. Mothers and siblings carried infants more than unrelated females.

When only the allomaternal data are considered (Table 5.3b), none of the sociodemographic variables accounted for variability in allonursing and carrying. Females that allonursed infants tended to carry them as well, but the effect of allonursing accounted for only 6.9% of the variability in the data. The association between allonursing

Table 5.3. Summary of Poisson regression analysis of the influence of sociodemographic variables on 2 maternal/allomaternal behaviors for the 1978 data. A. dataset includes mother-infant interactions, B. data excludes mother-infant interactions. Values are the % variance accounted for by each variable, total variance accounted for by the model, and significance of the residuals.

A.

INDEPENDENT VARIABLE	DF	NURSE	CARRY
R	1	62.5%	70.7%
Infant sex	1	8.5%	--
Total variance		71.0%	70.7%
Residual		sig.	sig.

B.

INDEPENDENT VARIABLE	DF	NURSE	CARRY
Nurse	1	--	6.9%
total variance		0.0%	6.9%
Residual		sig.	sig.

and carrying was as strong in 1977-78 as it was in 1986-88. Allonursing was more common in the earlier data (39 of 166 observed nurses) and appeared to be random in both data sets. Females nurse their own infants (if they have an infant) preferentially but will nurse other infants irrespective of kinship or dominance position.

The structure of Main group in 1977-78 was very different than it was in 1986-88. The group was composed of adult females primarily and most of the females had infants. Very few juvenile or young adult females were available for allomothering and these females carried their siblings preferentially. As a result, the mother-infant relationships dominate the data set. The contrast of results for carrying in the 2 data sets illustrates the importance of availability of allomothers in different age classes. That allonursing results were similar in the 2 data sets reflects the availability of lactating females and the willingness to nurse unrelated infants.

Residual Analysis

All of the Poisson regression analyses contained significant residuals after accounting for the significant sociodemographic variables. These residuals indicated that some interactions between females and infants occurred more or less often than predicted by the model. Large negative residuals occurred when specific females and infants interacted less than expected and indicate avoidance or

failure to gain access to an infant. Large positive residuals indicated that some females and infants interacted more than expected and indicate social preferences and special relationships between females and infants. I was interested primarily in the positive residuals as a means of identifying whether certain types of females were more likely to have strong relationships with infants than with other groups (Table 5.4).

In the 1988 data for maternal and allomaternal behaviors (Table 5.4), there are 3 classes of females with individuals that interact more with infants than predicted by the Poisson regression. Young-adult siblings, high-ranking old juvenile females, and low-ranking adult females all possess more large residuals, on a per female basis, than the other classes. Most of the moderate and strong residuals (31 of 35) occurred in dyads in Main group. This is most likely due to the absence of some classes of females in small groups and the tendency for female-infant interactions to be restricted to mothers and infants in small groups. The most active females in Main group included a high-ranking old juvenile with no siblings that was involved in 5 strong carrying and association relationships, a low-ranking adult that lost its infant at or shortly after birth and was involved in 4 strong allonursing and carrying relationships, and 2 young-adult females with siblings (all from the same matriline) that accounted for most of the

Table 5.4. Positive residuals for 1988 maternal and allomaternal behaviors and for 1978 maternal behaviors. Residuals are classed as between 1 and 2 standard deviations (SD) of the mean and as more than 2 standard deviations of the mean.

1988 Maternal/allomaternal

		Nurse		Carry		Associate	
Variable (n)		1-2 SD	2+ SD	1-2 SD	2+ SD	1-2 SD	2+ SD
Mother	(9)	2	-	1	-	1	-
Sibling	(9)						
yng juv.	(2)	-	-	1	-	-	-
old juv.	(2)	-	-	1	-	-	-
yng adult	(4)	-	-	1	2	1	1
adult	(1)	-	-	-	-	-	-
Other Female	(21)						
High Rank							
yng juv.	(2)	-	-	1	-	-	-
old juv.	(3)	-	-	3	2	1	2
yng adult	(4)	-	1	-	2	-	-
adult	(5)	-	-	-	-	-	-
Low Rank							
yng juv.	(1)	-	-	-	-	-	-
old juv.	(2)	-	-	1	-	1	-
yng adult	(1)	-	-	-	-	-	-
adult	(6)	-	3	-	3	1	3

Table 5.4 -- continued

1988 Allomaternal

Variable (n)		Nurse 1-2 SD	Nurse 2+ SD	Carry 1-2 SD	Carry 2+ SD	Associate 1-2 SD	Associate 2+ SD	Investigate 1-2 SD	Investigate 2+ SD
Sibling	(9)								
yng juv.	(2)	-	-	-	1	-	-	1	-
old juv.	(2)	-	-	-	-	-	-	-	-
yng adult	(4)	2	-	1	-	3	-	1	-
adult	(1)	-	-	-	-	1	-	-	-
Other Female	(21)								
High Rank									
yng juv.	(2)	-	-	1	-	-	-	-	-
old juv.	(3)	-	-	2	-	2	1	-	1
yng adult	(4)	1	-	-	1	-	-	-	1
adult	(5)	1	-	-	-	1	-	-	-
Low Rank									
yng juv.	(1)	-	-	-	-	-	-	-	-
old juv.	(2)	-	-	1	1	-	1	-	-
yng adult	(1)	-	-	-	-	-	-	-	-
adult	(6)	1	2	-	2	1	3	2	-

Table 5.4 -- continued

1978 Maternal/allomaternal

Variable (n)		Nurse 1-2 SD	Nurse 2+ SD	Carry 1-2 SD	Carry 2+ SD
Mother	(8)	1	1	3	1
Sibling	(2)				
yng juv.	(1)	-	-	1	-
old juv	(1)	-	-	1	-
Other Female	(12)				
High Rank					
yng juv.	(1)	-	-	-	2
old juv.	(1)	-	-	1	-
adult	(8)	3	1	-	1
Low Rank					
yng juv.	(1)	-	-	1	-
adult	(9)	2	-	-	-

carrying and association relationships. In Splinter group, the high-ranking old juvenile female was involved in a moderate association and carrying relationship with a low-ranking infant. These females are said to be involved in special relationships with infants because the residuals are consistently positive over 2 or more behaviors or because the residuals are greater than 2 SD above the mean. The lack of significant residuals for the mother-infant interactions indicates that the models adequately accounts for maternal behavior. The models also account for most of the sibling-infant interactions (except for young adult sisters).

The results for allomaternal interactions confirm the results of the first residual analysis (Table 5.4b). Young-adult siblings, high-ranking old juveniles and low-ranking adult females are more likely to be involved in special relationships as determined by the pattern of residuals.

In the 1978 data (Table 5.4c), most of the large residuals are associated with adult females, reflecting the structure of Main group in 1978. The models account for much of the variation in maternal behaviors. Some mothers carried infants more often than others. One infant was born crippled and was carried often by its mother and 2 juvenile siblings. The strong residual for mother infant-carrying was for a particularly small female infant that also engaged in allomaternal nursing from 6 different females in addition to her mother. Most of the large residuals in allomaternal

behaviors occurred between adult females and unrelated infants. High-ranking adult females allonursed low-ranking infants more than low-ranking females allonursed high-ranking infants. All of the residuals for high-ranking adult females are attributed to the dominant female. She nursed 6 infants in addition to her own, including 1 infant that nursed almost half as often as her own infant. The residuals for allomaternal behaviors in 1978 are not presented because the model for carrying was so weak (accounting for only 6.9% of the variation).

In summary, the residual analyses indicate that much of the variability not accounted for by the regression models is due to special relationships by particular individuals within the sociodemographic classes. Some of these females appear to be attracted to infants in general whereas others appear to be attracted to particular infants. Characteristics of individual infants, also may influence female-infant interactions; an infant may be more attractive to a female or require or demand more attention from females.

Discussion

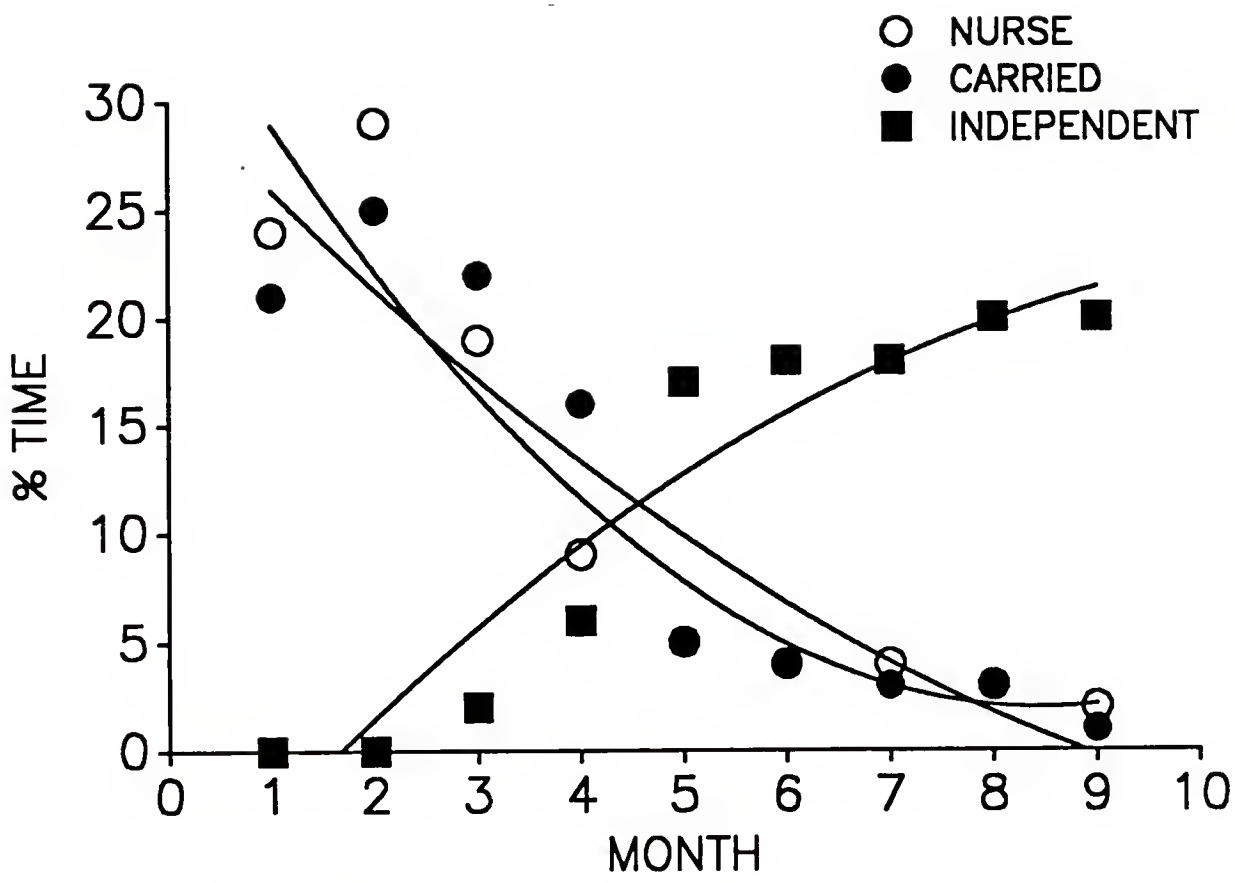
Timing of Infant Care

C. olivaceus infants are born weighing only 8.5% of the mother's weight and possessing poorly developed hindquarters (Freese and Oppenheimer 1981). Mothers are the sole care givers in the first 3 months and account for almost all of

the infant care observed. Of the total maternal care observed, 36% occurred in the first 3 months whereas in the second 3 months, this figure dropped to 18.3%. More than half of the maternal carries were observed in the first 3 months; only 23% occurred during the second 3 months. During the third month, the infant begins exploring its surroundings (Fig. 5.2; Levy 1981) and the time spent in close association with the mother decreases rapidly thereafter. By month 5, the infant is essentially independent of its mother for locomotion and the rate of nursing is decreasing rapidly. Infants are independent of the mother and rarely nursing by month 8.

During the third through sixth months, the role of the allomother is especially pronounced; 42% of all allomaternal interactions and 79% of allomaternal carrying occur at this time. Allomothers assume much of the infant carrying and babysitting activity at this time and allomaternal interactions exceed maternal interactions (17.1% vs 11.0% of all female-infant interactions). Clearly, allomaternal care is an essential component to infant care during the critical time period when the infant is developing independence from its mother. The high level of allomaternal care (38.8% overall) and the timing of the onset and peak of allomaternal care indicate that such care is also essential to infant survival. A conclusive link between infant survival and infant care would require an analysis of

Figure 5.2. Percent of time infants spent nursing, being carried by mother, and independent of mother in the first 9 months of life for 2 captive infants.



data source: Levy 1981

monthly survival rates for a group of infants as well as monthly estimates of the amount of maternal and allomaternal care received. This study establishes that allocare accounts for a large portion of infant care and the timing of allocare assures a high level of infant care at a time when maternal care is declining.

Effect of Kinship

Relatedness is the most consistent influence on maternal and allomaternal behavior in C. olivaceus. Mothers and siblings interact with infants more than distant kin, and distant kin interact with infants more than nonkin. Part of this is attributed to the obvious effect of mother-infant relationships, but kinship remains the most consistently significant effect after removing maternal relationships. Siblings participate in allomaternal behaviors almost 4 times as often as distant kin and nonkin. Siblings are more likely to be involved in carrying infants and association; behaviors that permit the mother time to engage in activities, such as foraging, unencumbered by an infant. These behaviors also are the most common allomaternal interactions. Siblings are involved somewhat in allonursing but this is a behavior restricted to lactating females and appears to be random. Distant kin and nonkin investigate infants more but siblings are the second most active category of investigating females (see below).

Siblings, especially the younger age classes, were often prevented from investigating the infant by the mother. The mother would move away from a daughter (as she would if trying to avoid a higher-ranking female that attempted to investigate) or, occasionally, would slap or bite the daughter. Usually a daughter gained access to the infant by grooming her mother or through persistent approaches. It appeared that the mother, although tolerating investigation of the infant, sought to avoid investigations. I could not, however, detect any obvious sign of stress during this behavior, except that the mother would move when approached by a daughter or high ranking female. Because the mother resists or avoids investigation of its infant when possible, The interaction appears to be dependent on mother and investigator, rather than infant and investigator. It may be more appropriate to consider investigation behavior separately from allomaternal behaviors in which the infant is an active participant.

In a review of maternal and allomaternal care, Nicholson (1986) cited 7 studies in which siblings participated in allocare more than non-siblings, and 2 studies in which kin interacted less. In evaluating these studies, however, Nicolson found that for savannah baboons, rhesus macaques, Japanese macaques and chimpanzees, the amount of time infants spent with allomothers was low (under 10%). Hrdy (1977) has argued that relatedness is not an

important factor in allomother care in Hanuman langurs, primarily because the attractiveness of kidnapped infants suggested that any infant was attractive to any female and the effect of relatedness could not be discerned from privileged access (shared by kin and higher ranking females). I agree that infants may be attractive to females irrespective of kinship, but this cannot be taken as evidence against the effect of relatedness. Most allomaternal interactions occurred within the social units and relatedness was unknown in Hrdy's study except for 2 sibling-infant dyads. Hrdy's findings of privileged access and age effects are similar to those of other studies, but the question of kinship was not adequately addressed.

Effect of Female Rank

High-ranking females interacted more with infants than low-ranking females when the infant was distantly related or unrelated. This effect was consistent (but not absolute) across age classes of females and across behaviors. This suggests that high-ranking females had more access to infants of low-ranking mothers and the results for investigation behavior support this idea. Low-ranking females did not approach higher-ranking females with infants, daughters had limited access to infants, but high-ranking females approached and investigated infants freely. In contrast to many studies (see Hrdy 1977; Cheney 1978; Silk 1980; Altmann 1980; Lee 1983) infant abuse played no

role in rank-related interactions. Female abuse of infants was so rare during the study that it could not be included in analysis. Furthermore, only sisters were abusive to infants and the abuse took the form of trying to remove an infant from a female's back. Infants of high-ranking females were not more attractive than low-ranking infants. It appears that the major determinant of interaction with infants was whether a female had an infant of its own or a sibling infant to interact with.

Low-ranking females had low rates of interaction with infants. This may be due to the spatial distribution of females in the group in relation to rank and the position of semi-independent infants. Robinson (1981) showed that infants tend to be clustered in the center of the group during foraging and group movements. Low-ranking females are usually restricted to the periphery of the group and may not have the opportunity to interact with infants. High-ranking females, by contrast, are positioned in the center and front of the group and are therefore in a spatially advantageous position to interact with infants. Although it is impossible to distinguish lack of interest from lack of access using the data presented here, there is no a priori reason to expect differences in infant attractiveness to females of different rank. Low-ranking females exhibit lower rates of affiliative interaction than high ranking females (see

O'Brien Chapter 2) and this may extend to allomaternal interactions as well.

Effect of Age

Although there is a significant effect of female age in this analysis, it is relatively minor when the effects of relatedness and rank also are considered. Old juvenile and young adult females interact more than expected, adult females interact less than expected, and young juveniles interact approximately as expected. This pattern is similar to those of other studies (Lancaster 1971; Hrdy 1977; Chism 1978, Nicholson 1986, Horwich and Gebard 1986) and is thought to result from the need for young primates to acquire skills as mothers (Lancaster 1971; Hrdy 1977; Altmann 1980). Young juveniles are attracted to infants but often are unable to gain access in the early months. This may be due to the interference of older females who do most of the carrying of young infants, or to the inability of young juveniles to carry infants adequately because of small size and/or inexperience. Interference by older females is more likely because young juveniles participate in carrying more as the infant grows. The high degree of altriciality of infants may require more skill in carrying than a young juvenile is capable of. By carrying older infants, that are less susceptible to careless handling, young juveniles may gain initial experience in allocare.

The most active allomothers are the old juvenile and young adult females. These females are nulliparous or primiparas that lost infants at birth (1 female) and are very attracted to infants. The least active allomothers were the adult females. Again, this is the pattern observed in many studies of allocare, especially those studies in which all age classes are represented. Old juveniles and young adults are the females that express the most interest in infants, carry infants at an early age and associate with infants of all ages. Younger females are more likely to be related to infants than adults, are likely to gain more experience than adults by interacting with infants and are least likely to have an infant of their own to care for. Young females also are more likely to have future interactions with infants as infants become active group members.

That allomaternal care is affected by the presence of females in different age classes is illustrated by the differences in age distribution of females in the 1977-78 and 1986-88 data. In 1977-78, 75% of females in Main group were adults and 17% were young juveniles and 8% were old juveniles. Adult allomothers carried infants 10% and the juveniles carried 41% of the time. This is compared to 1986-88 data for 3 groups, when 55% of females were adults, 20% were young adults, and 25% were juveniles. Adult allomothers carried infants 2.9%, young adults carried 7.5% and

juveniles carried 12.4% of the time. The inclusion of small groups with few allomothers in 1986-88 and the presence of a wider range of age classes resulted in very different profiles of carrying interactions.

Allomaternal Nursing

Allomaternal nursing departed from the patterns described above for other allomaternal behaviors. It was an infrequent behavior compared to the others, involved only adult, lactating females, and was not influenced by rank or kinship. Infants nursed from unrelated females and from higher ranking as well as lower ranking females. Females facilitated these nursing interactions by raising the arm to expose the nipple, as they would when their own infant approached to nurse. Not all infants and adults participated in allonursing but the behavior was widespread and appears to be a general phenomenon among C. olivaceus.

Allomaternal nursing is a rare behavior in primates in general. Jay (1962) reported that female P. johnii would allow a newborn infant to suckle, whether the female was lactating or not, as a means of reducing stress to the infant. The use of a nipple as a pacifier may facilitate early infant transference. Poirier (1968) observed that P. johnii females engaged in babysitting showed no preference for nursing their own versus other females' infants. Hrdy (1977), however, observed no allomaternal nursing in P. entellus, although they exhibited early infant transfer. Few

other examples of allomaternal nursing in primates exist (but see van Wulfften Palthe and van Hooff 1976).

In P. johnii, as in C. olivaceus, allomaternal nursing appears to be indiscriminate. It is possible that allonursing is a form of reciprocal behavior, but one that is exchanged between adult females via the infant being nursed. If a female engages in allonursing with a high probability that her own infant will nurse from other females, then the cost to the mother (lost milk) will be compensated by her infant's allonursing. This situation would qualify as a reciprocal relation between females with payment in kind (Bertram 1982) for an apparently altruistic act. Such a situation, furthermore, would explain why allomaternal nursing extends across rank and kin lines, and includes pregnant females and females that recently lost their infants. All females must, on the average, participate in allonursing for an indiscriminant system to evolve. If all females are prone to participate in allomaternal nursing, then females that were pregnant or recently lost infants would also be expected to participate; their payback would be delayed but expected in future reproductive effort. Such indiscriminant nursing (independent of relatedness and rank) also occurs in the colonial nurseries of Mexican free-tailed bats (Tadaria brasiliensis; Davis et al. 1962) and long-winged bats (Miniopterus schreiberii; Brosset 1962) but has not been well documented in other mammals.

Maternal Care and the Evolution of Allomaternal Care

Infant care is a complicated phenomenon involving mothers, infants, and other females; composed of several behaviors that have different costs and benefits associated with them; and influenced by a number of sociodemographic characteristics of the interactants and the groups in which they live. Since there are variable energetic costs associated with behaviors such as nursing, carrying infants, associating with infants, and investigating infants, there must be benefits to the interactants involved. Why would a mother give up an infant if the infant is at risk of mortality as a result? Why does an infant interact with allomothers when its own mother is in the group? Why do allomothers help?

A mother benefits from allomaternal care of its infant if the care results in a reduction of the energetic cost of maternal care and benefits the infant. Lactation is energetically very costly (Millar 1977). Carrying an infant is a cost that increases as the infant grows. A threshold must exist at which infant care becomes so energetically costly that the female is at risk of increased mortality (Altmann 1980). The consequence of a mother's mortality usually includes the death of the dependent infant because adoption and allonursing are rare in primates (Nicholson 1986). If infant care increases female mortality (thereby putting the infant at risk), then selection should act to

accelerate infant independence to reduce maternal costs. The results presented here suggest that the availability of allomothers permits the mother to reduce her investment in infant care by reducing the cost of carrying, babysitting, and lactation. The onset of allocare while the infant is still highly dependent assures a sustained level of infant care while reducing maternal care.

How does the allomother benefit through incurring the costs of allomaternal care? Young allomothers may benefit by gaining experience at mothering (Epple 1975; Hrdy 1977; Hoage 1978) and by promoting increased group size because female fecundity is higher in larger groups (Robinson 1988b). Adult allomothers benefit less than young allomothers because they know how to care for infants and they are less likely to survive to enjoy future benefits. Allomothers of different ranks may benefit differently when the costs of a behavior are rank related rather than energetic (as in investigation). Related allomothers benefit by gaining experience, by the survival of additional group members and through inclusive fitness (Hamilton 1964; Brown 1987).

The data presented here suggest that kinship is the dominant influence on the degree of allomaternal care in capuchin monkeys. Females investigated, carried, and associated with siblings preferentially, and invested more time and energy in allocare than did unrelated or distantly

related females. Lactating females participate in allonursing of siblings as well as others. A female's age and rank influence which behaviors the female engaged in. The unrelated, high ranking females investigate and associate. Unrelated, low ranking females carry and associate, but generally have little access to unrelated infants. It appears that unrelated, high ranking females invest less than siblings and participate in less costly behaviors (investigate versus carry) than low ranking females. Adult females participate in allomaternal care less than young adult and juvenile females. Among unrelated females, adults associate and investigate whereas juveniles carry and associate. These results are consistent with the idea that younger females benefit more than older females from allomaternal care. The exception to these patterns is allomaternal nursing that appears to be indiscriminant. Kinship determines the level of care given; age and rank influence the type of care given by allomothers.

CHAPTER 6

CONCLUSION

This study has demonstrated the complexity of social behavior in female wedge-capped capuchin monkeys, Cebus olivaceus. Capuchin monkeys engage in a wide variety of social interactions including grooming, supplantation, fighting, agonistic support, and allomaternal care of infants. Group size and composition, dominance rank, matrilineal relatedness, and age affect the expression of these behaviors, and the choice of a partner or a victim. It is through social interactions that relationships are established among group members and social structure is maintained. No single parameter adequately explained social behavior; the interaction of demography, dominance rank and relatedness must be considered.

Females associated more with other females than with males. When associating with males, females preferred to associate with the dominant male over subordinate subadult males. When associating with other females, choice of partner was a function of the relative ranks of the females, the females' ages, their matrilineal relatedness, and the history of interactions between the pair. Patterns of social

interactions, however, did not reflect simply patterns of association. Some pairs of females had predominantly affiliative relationships, some had uniformly antagonistic relationships, and others had relationships that reflected a balance between affiliation and aggression.

Group size and structure had a fundamental effect on female social interactions in this study. Females in the large group were in close association with and interacted with other group members more than females in the small groups. Females in the large group groomed more on average and the grooming sessions tended to last longer than in small groups. Aggression among females and between females and males was significantly higher in the large group. Females in the large group interacted with infants other than their own, and associated with and groomed the dominant male more often in the large group than in the small groups.

Some of the differences noted above can be attributed to differences in group structure. As the number of individuals in different age-sex classes change, rates of social behaviors also change. The addition of 1 subadult male to a small group caused a major increase in rates of aggression toward males compared to a group without subadult males. Male aggression toward females was due primarily to the presence of subadult males. Group structure also affected the availability of allomothers in large and small groups. As the number of nulliparous adult and old juvenile

females increased, more potential allomothers of the optimal age were available. In groups with few potential allomothers, males may increase their participation in allocare. Finally, the number of additional matrilines and females within matrilines was associated with increased rates of affiliative behavior within matrilines and increased rates of aggression between matrilines.

I have shown that the relatedness of interactants is important for social relationships with females and with infants. Females associated more with related females than with unrelated females. Females groomed related females relatively more often than unrelated females. Within matrilines, females groomed more with mothers than with female siblings. Females directed more allomaternal care toward infant siblings than toward unrelated infants. Sisters carried infants and associated with infants more than unrelated females. Females were less aggressive toward related females. Relatedness with males was less important in social interactions between males and females. This may be because males emigrate from the group at an early age and relatedness between males and females, therefore, is low. There is some evidence, however, that affiliative behavior toward subadult males may be directed toward young males born in the group. These males either have related females or familiar peers in the group.

Female age had minor effects on relationships with other females and infants, but not with males. Age did not affect patterns of association among females or between females and males, but it did influence association with infants. Old juvenile and young-adult females participated in allomaternal care more than parous adults and young juveniles, but female age was relatively unimportant to allomaternal care compared to effects of relatedness and rank. These females usually were caring for siblings. Age affected patterns of fighting and supplantation among females, but the effect was slight. Adults were most aggressive among themselves, young adults were equally aggressive toward all age classes and juvenile females were least aggressive. Adult females groom preferentially among themselves. When juveniles groom adults, the adults tend not to reciprocate grooming. The influence of age appeared strongest in peer group interactions. Adults did not interact as often with juveniles as they did among themselves. Because juveniles are in the process of establishing themselves in the social network of the group, peer interactions are important for determining future social position. Interactions between adults and juveniles may benefit juveniles more than adults and the adults show less interest in interactions with juveniles.

Female dominance rank exerted a major effect on interactions with infants, with males and with other

females. Females that outranked the infant's mother investigated infants and associated with infants more than lower-ranking females. Lower-ranking females and siblings carried infants more. Dominance rank also affected access to the dominant male. Only high-ranking females formed close affiliative relationships with this male; middle- and low-ranking females were rarely associated with or groomed the dominant male. Subadult males rarely were aggressive toward high-ranking females, because these females retaliated with aggression. Most aggressive interactions and supplantations involved middle- and low-ranking females.

Female-female relationships were structured on rank as well as on matrilineal relatedness. High- and medium-ranking females associated more among themselves than with low ranking females. High-ranking females initiated grooming more often, groomed longer and more frequently, and terminated grooming sessions less frequently than low-ranking females. All of the close grooming relationships occurred among high-ranking females or among the 2 high-ranking matrilines in the large group. Aggression was most frequent among high- and medium-ranking females. Low-ranking females were victims of supplantation more than aggression because they usually avoided other animals except during foraging periods when they were easily supplanted by higher-ranking females. Much of the fighting occurred in a nonforaging context between females of similar ranks. Such

social fighting may serve to reinforce relative dominance ranks.

Much of the variability in female social behavior of wedge-capped capuchin monkeys is attributed to individual differences. This variability is important even after effects of demography and social structure are removed. It is expressed generally as personality differences such as the propensity to fight, willingness to groom another, or withdrawal from social interactions. Individual variability is also expressed in specific dyadic relationships such as the preference of a dominant female for a particular low-ranking female when she is aggressive toward all other low-ranking females. Variability in dyadic relationships may develop during the time that juveniles form relationships and persist into adulthood. A female may develop a close affiliation with another through allomaternal interactions or may develop aggressive peer relationships. These relationships then become permanent features of the social interactions of a group. Such seemingly anomalous relationships impair attempts to make generalizations about the determinants and consequences of social structure. It is only through the longterm study of a large number of individuals that we will understand the present anomalies of individual variability.

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BIOGRAPHICAL SKETCH

Timothy G. O'Brien was born on May 6, 1955, in Ashtabula, Ohio. He received his B.S. in forestry and wildlife from Virginia Polytechnic Institute and State University, where he studied physiology and toxicology, and worked on a variety of field projects. In 1978, he moved to North Carolina State University where he earned a M.S. in wildlife biology for his work on the American alligator in North Carolina, and a M.Stat. in statistics. In 1985, he moved to Gainesville to study the social behavior and demography of capuchin monkeys under Dr. John G. Robinson.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

John G. Robinson, Chair
Associate Professor of Forest Resources and Conservation

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

John F. Eisenberg
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This dissertation was submitted to the Graduate Faculty of the School of Forest Resources and Conservation in the College of Agriculture and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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